

EXALLODONTUS AGUANAI, A NEW GENUS AND
SPECIES OF PIMELODIDAE
(PISCES: SILURIFORMES) FROM DEEP RIVER
CHANNELS OF SOUTH AMERICA, AND
DELIMITATION OF THE
SUBFAMILY PIMELODINAE

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Abstract.—A new genus and species of pimelodid catfish, *Exallodontus aguanai*, is described from the deep channels of the Orinoco and Amazon rivers. This taxon is diagnosed by autapomorphically robust jaw teeth reduced to 2–3 rows, and an obtusely triangular “lacrimal” (=infraorbital 1+2). Also, this taxon has a unique combination of phylogenetically advanced characters—long adipose fin, short dorsal-fin spine, short head, very small eye, vertical neural spines on middle vertebrae, sharply ridged supraoccipital process, paddle-like anterior anal-fin rays, and transversely oriented posterior nares.

The subfamily Pimelodinae is circumscribed to include 32 nominal genera: *Aguarunichthys*, *Bagropsis*, *Bergiaria*, *Brachyplatystoma*, *Calophysus*, *Cheirocerus*, *Conorhynchus*, *Duopalatinus*, *Exallodontus*, *Goslinia*, *Hemisorubim*, *Hypophthalmus*, *Iheringichthys*, *Leiarius*, *Luciopimelodus*, *Megalonema*, *Merodontodus*, *Perrunichthys*, *Parapimelodus*, *Paulicea*, *Phractocephalus*, *Pimelodina*, *Pimelodus*, *Pinirampus*, *Piramutana*, *Platynematachthys*, *Platysilurus*, *Platystomatichthys*, *Pseudoplatystoma*, *Sorubim*, *Sorubimichthys*, and *Steindachneridion*. This subfamily is supported by three synapomorphic characters—the dendritic arrangement of lateral line system on the head and nape, an elongated lateral ethmoid-palatine condyle, and a sutural joint between the fifth and sixth centra. Within the Pimelodinae three nested subgroups are delineated and diagnosed but not named formally: (1) “Group A,” comprising all pimelodines except *Phractocephalus*, *Leiarius* and *Perrunichthys*; (2) “*Calophysus-Pimelodus* clade” that includes Stewart’s (1986a) “*Calophysus* group” (*Calophysus*, *Pinirampus*, *Pimelodina*, *Luciopimelodus* and *Aguarunichthys*) plus *Megalonema* plus our third group; (3) “*Pimelodus* group” composed of the nominal genera *Bagropsis*, *Bergiaria*, *Cheirocerus*, *Conorhynchus*, *Duopalatinus*, *Exallodontus*, *Iheringichthys*, *Parapimelodus*, *Pimelodus*, *Platysilurus*, and *Platystomatichthys*. Variations of the trigeminofacial nerve foramina are described in relation to a possible phylogenetic diagnosis of *Pimelodus*.

Resumen.—En este trabajo se describe a *Exallodontus aguanai*, un nuevo género y nueva especie de bagre pimelódido proveniente de los canales profundos de los ríos Orinoco y Amazon. *Exallodontus* se reconoce por dos caracteres autapomórficos: (1) dientes mandibulares robustos y reducidos a 2 ó 3 filas, y (2) presencia de un lacrimal (infraorbitario 1+2) triangular con ángulos obtusos. Este taxon tiene, además, una combinación única de caracteres filogenéticamente avanzados—aleta adiposa larga, espina de la aleta dorsal corta, cabeza relativamente pequeña, ojo muy pequeño, espinas neurales verticales en las vértebras localizadas hacia la mitad de la columna, processo

supraoccipital con una cresta pronunciada, radios anales anteriores en forma de paleta, y narceas posteriores orientadas transversalmente.

La subfamilia Pimelodinae se ha restringido para incluir los siguientes 32 géneros nominales: *Aguarunichthys*, *Bagropsis*, *Bergiaria*, *Brachyplatystoma*, *Calophysus*, *Cheirocerus*, *Conorhynchos*, *Duopalatinus*, *Exallodontus*, *Goslinia*, *Hemisorubim*, *Hypophthalmus*, *Iheringichthys*, *Leiarius*, *Luciopimelodus*, *Megalonema*, *Merodontodus*, *Perrunichthys*, *Parapimelodus*, *Paulicea*, *Phractocephalus*, *Pimelodina*, *Pimelodus*, *Pinirampus*, *Piramutana*, *Platynematachthys*, *Platysilurus*, *Platystomatichthys*, *Pseudoplatystoma*, *Sorubim*, *Sorubimichthys*, y *Steindachneridion*. Esta subfamilia está definida por tres caracteres sinapomórficos—organización dendrítica de los canales del sistema de la línea lateral en la cabeza y la nuca, cóndilo palatino del etmoides lateral alargado, y una unión sutural entre los centra de la 5a. y 6a. vértebras. Entre los Pimelodinae se delimitan tres subgrupos o clados que son aquí definidos, pero a los cuales no se les asigna ningún nombre formal: (1) “Grupo A,” que abarca a todos los Pimelodinae con la excepción de *Phractocephalus*, *Leiarius* y *Perrunichthys*; (2) un “clado *Calophysus-Pimelodus*” que incluye el “grupo *Calophysus*” de Stewart (1986a), es decir, *Calophysus*, *Pinirampus*, *Pimelodina*, *Luciopimelodus* y *Aguarunichthys*, más *Megalonema* y nuestro tercer grupo, (3) un “grupo *Pimelodus*” formado por los géneros nominales *Bagropsis*, *Bergiaria*, *Cheirocerus*, *Conorhynchos*, *Duopalatinus*, *Exallodontus*, *Iheringichthys*, *Parapimelodus*, *Pimelodus*, *Platysilurus*, y *Platystomatichthys*. Finalmente, se describen las variaciones de los forámenes del nervio trigéminofacial en relación con una posible diagnosis filogenética de *Pimelodus*.

During the Catherwood Foundation Peruvian-Amazon Expedition in 1955, personnel from the Academy of Natural Sciences of Philadelphia made a collection of fishes in the Río Marañón using a small trawl. Böhlke (1970:2) reported that this collection contained some unusual catfishes and he urged “that more bottom sampling should be attempted in the large South American rivers.” Later, in 1978 and ’79, bottom trawling operations from R/V *Eastward* and smaller craft in the deep river channels of the lower Orinoco yielded a surprising diversity and biomass of fishes (López et al., 1985). These achievements stimulated the use of bottom trawls in other large Neotropical rivers in Venezuela, Colombia, Brazil, Panama and Ecuador. The most significant result of these efforts has been the discovery of an abundance of catfishes and electric fishes in the deep chan-

nels, with many distinctive species apparently restricted to this habitat (Mago-Leccia et al. 1985; Lundberg & Stager 1985; Lundberg & Mago-Leccia 1986; Stewart 1985, 1986b). In this paper we describe a distinctive pimelodid catfish that is known only from deep trawl samples—*Exallodontus aguanai*.

In treating the interrelationships of *Exallodontus* we reconsidered some higher level groups of pimelodid catfishes. Recently, a few well-characterized monophyletic groups of pimelodid species and genera have been delimited (Stewart 1986a, Lundberg & McDade 1986, Lundberg et al. 1988, Ferraris 1988). Two pimelodid subfamilies, Rhamdiinae and Pseudopimelodinae, have been diagnosed within an explicit phylogenetic framework (Lundberg et al. 1991). From these alignments of genera it has been possible to more precisely diagnose and re-



Fig. 1. Diagram of phylogenetic interrelationships of pimelodine catfishes and informal subgroup names used in this paper. Bold lines highlight the higher clades to which *Exallodontus* belongs.

strict the membership of the heretofore vague subfamily Pimelodinae (see Fig. 1 and below).

Methods.—Counts and measurements are those described by Lundberg & McDade (1986). In addition, prepectoral-fin length is the distance from snout tip to base of pectoral spine, and interocular distance is the least distance between dorsal margins of fleshy orbital rims. All measurements are straight-line made with dial calipers held directly on the fish. Measurements and counts in the tables are those for both sexes combined. Measurements in materials list are standard lengths in mm, unless noted otherwise. Gill rakers, branchiostegal rays and vertebrae were enumerated on cleared

and stained specimens, dry skeletons and radiographs. Total vertebral counts include five for the Weberian complex and one for the compound caudal centrum (fused preural centrum 1 + ural centra). The first caudal vertebra is the most anterior one with a full hemal spine that is subequal in length to the following spine.

Institutional abbreviations follow Leviton et al. (1985).

In phylogenetic analysis, polarization of character transformation series into primitive (plesiomorphic) and derived (apomorphic) conditions is based on outgroup comparisons to other pimelodid groups (see Comparative pimelodid material examined) following the partly resolved hypoth-

esis shown in Fig. 1 (Lundberg & McDade 1986; Lundberg et al. 1988, 1991), plus other catfish groups (see Comparative non-pimelodid materials examined) with the Diplomystidae and the fossil †Hypsidoridae taken stepwise more inclusively as the sister groups to other catfishes (Grande 1987).

Exallodontus, new genus

Figs. 2–10, 13, Tables 1–3

Type species. — *Exallodontus aguanai*, new species.

Diagnosis. — A genus of catfishes distinguished from other Pimelodidae by two uniquely derived features: (1) 2–3 rows of heavy, firmly attached conical teeth on premaxillae and dentaries (Fig. 2); (2) “lacrima” (=infraorbital 1+2 in this and other Pimelodinae, see below) shaped as an obtuse-angled triangle with nearly straight sides (Fig. 3).

Exallodontus is further distinguished from other pimelodid genera by having a unique combination of features whose phylogenetic generality is not yet fully determined. These features are useful for identifying the new taxon and will be of value in future comparative studies of the family. These are: (3) relatively long, nearly straight-margined adipose fin (adipose fin length contained 2.0–2.5 in SL, Fig. 5); (4) short dorsal fin spine and low dorsal fin (dorsal-fin spine length contained 5.6–8.6 in SL, Fig. 5); (5) relatively small head (head length contained 4.0–5.2 times in SL, Fig. 5); (6) a relatively small eye (horizontal eye diameter contained 3.4–5.5 times in snout length, 7.4–12.0 times in head length, Fig. 5); (7) neural spines of vertebrae 13 (or 14) to 23 (or 24) oriented 90° to horizontal axis of centra (Fig. 4); (8) supraoccipital process with a narrow median keel above somewhat concave sides (Fig. 6A), markedly angular in cross-section, slender and tapering to its peg-and-socket joint with supraneural (basal width of supraoccipital process about 2 times in length); (9) anterior anal-fin rays broadened, forming a paddle-like blade (Fig. 7); (10) poste-

rior nostril ovoid, with its long axis oriented transversely (Fig. 7).

Comparison. — The foregoing diagnostic features of *Exallodontus* are here compared to similar pimelodid taxa.

1. Dentition of jaw bones (Fig. 2): Generally in catfishes, including most pimelodids, the jaw teeth are in bands with many more than three irregular rows (e.g., Lundberg & McDade 1985:figs. 6, 9), and the teeth are slender, conical, and at least slightly depressible. There are a few pimelodids, however, that have, like *Exallodontus*, a reduced number of tooth rows, but in each case the shape or arrangement of the teeth is very different. *Calophysus macropterus* has two rows of teeth on the premaxillae and a single row on the lower jaw. The outer premaxillary and dentary teeth of *Calophysus* are uniquely incisiform with minutely scalloped edges, and their spacing is highly regular. *Pimelodina flavipinnis* has one or a few rows of weakly attached, very fine teeth on the jaw bones (Stewart 1986a:fig. 1c). *Cheirocerus* (Stewart & Pavlik 1985:fig. 2) and *Iheringichthys* spp. may have single rows or small patches of weak premaxillary teeth in young that are lost with growth, and a single row on the lower jaw. Except for *Calophysus*, the dental conditions of these pimelodids seem clearly to be reductive, unlike the much heavier dentition of *Exallodontus*. The conditions possessed by *Pimelodina*, *Cheirocerus*, *Iheringichthys* and *Calophysus* are clearly apomorphic among pimelodids, but the striking differences between them and *Exallodontus* suggest that they are not homologous.

In respect to tooth shape and attachment, we have found that *Pimelodus altissimus* have jaw teeth that are nearly as strongly developed and firmly anchored as those of *Exallodontus*, but *P. altissimus* has 6–8 premaxillary and dentary tooth rows. The similarity between these two species in tooth shape is possibly a synapomorphy.

2. Shape of anteriormost infraorbital or “lacrima” bone (Fig. 3): The anteriormost infraorbital bone in *Exallodontus* and many

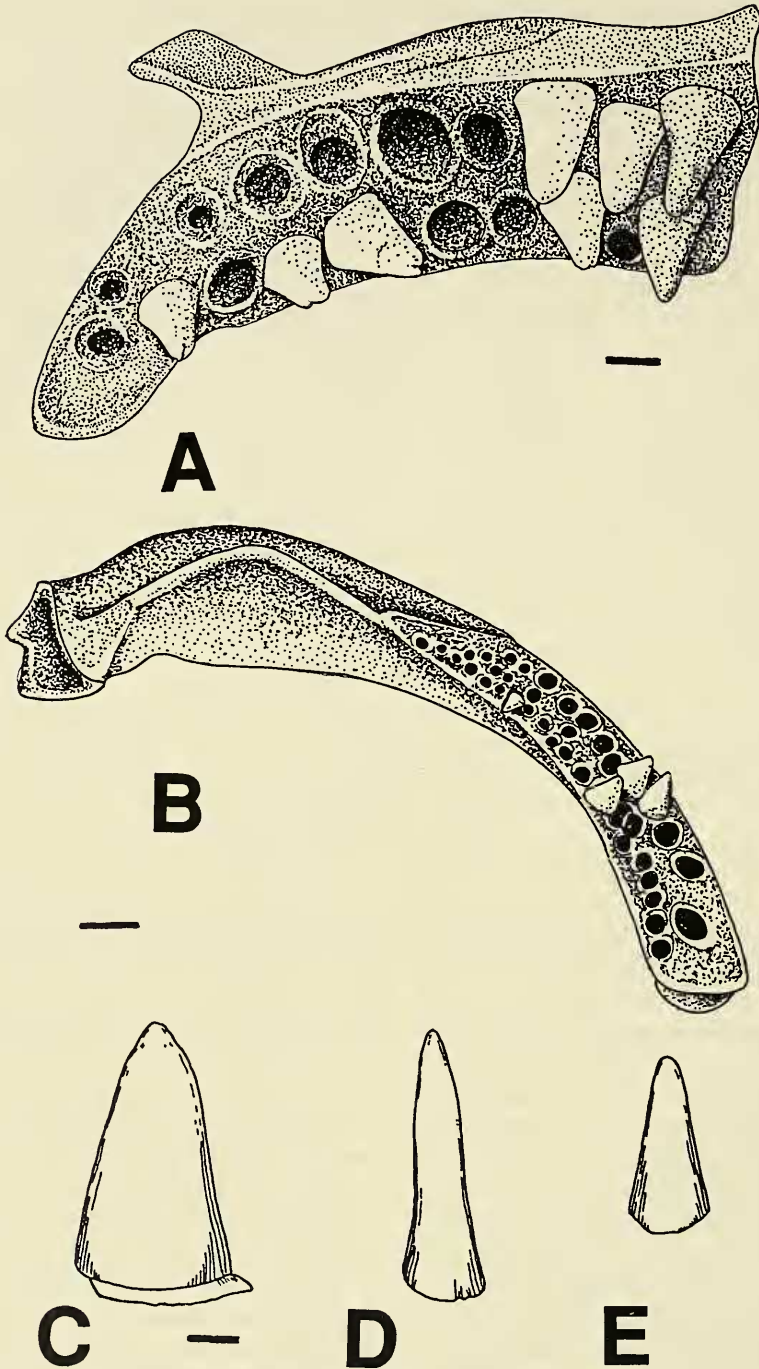


Fig. 2. Jaw bones and dentition of *E. aguanai*. A. Right premaxilla in ventral view, MBUCV-V-ES112, B. Left dentary in dorsal view, MBUCV-V-ES112, C-E. Middle outer row, dentary teeth from comparably sized specimens of C. *E. aguanai*, DU-F-977, 166 mm SL, D. *Pimelodus grosskopfi*, DU-F-919, 211 mm SL, E. *Pimelodus altissimus*, AMNH 40138, 121 mm SL. Scale bars for A = 1 mm, B = 0.5 mm. Single scale bar for C-E = 0.25 mm.

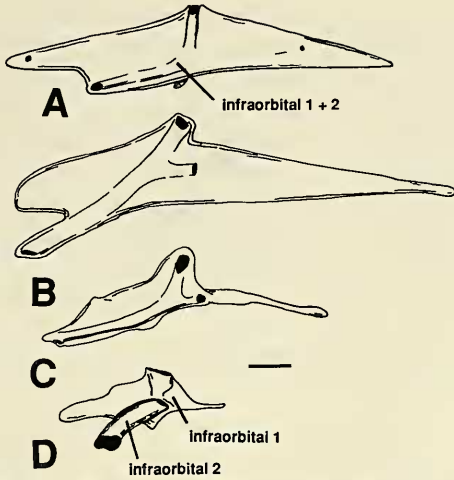


Fig. 3. Right lateral views of infraorbital bones 1 (=lacrimal) and 2 of: A. *E. aguanai*, DU-F-977, B. "*Pimelodus A*" from the Orinoco DU-F-1006, C. *P. pictus*, DU-F-1012, D. *Pimelodella chagresi*, USNM uncat. (Field No. WCS1530, Panama). Single scale bar for A-C = 0.5 mm, for D = 1.0 mm.

other pimelodids is compound because of fusion between the first and second infraorbital. In most other catfishes, including the "rhamdiine" pimelodids (Lundberg et al. 1991), the second infraorbital is a small, tubular lateralis ossicle that lies laterally adjacent to the posteroventral corner of the first (Fig. 3; see also Lundberg & McDade 1985:fig. 7). Both the compound infraorbital and the separate first and second infraorbitals primitively have a tetradiate form: anterior and posterior processes of the first infraorbital lie along the margin of the olfactory capsule between the premaxilla and lateral ethmoid, a dorsal process continues the tubular lateralis component that traverses the first infraorbital, and the second infraorbital projects posteroventrally. Uniquely, in *Exallodontus* additional ossification between the four processes creates the triangular and nearly straight-edged form of this bone.

3-6. Morphometric characters: Compared to other generally similar pimelodids *Exallodontus* possesses a relatively small eye

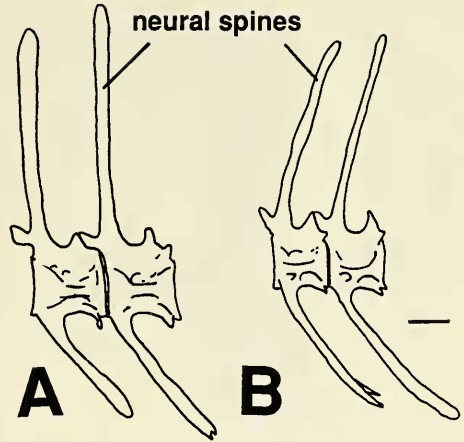


Fig. 4. Left lateral views of mid-body vertebrae of A. *E. aguanai*, vertebrae 16 and 17, DU-F-977, B. *Pimelodus grosskopfi*, vertebrae 17 and 18, DU-F-919. Scale bar = 2.0 mm.

and head, low dorsal fin and long adipose fin (Fig. 5).

7. Angle of neural spines (Fig. 4): With only slight variation, in *Exallodontus* the neural spines of vertebrae 13 or 14 to 23 or 24 are oriented at 90° to the horizontal axes of their centra. Vertically oriented neural spines on the mid-body vertebrae are also present in an undescribed Orinocan species that we informally refer to as "*Pimelodus A*." (In Eigenmann & Eigenmann [1890] "*Pimelodus A*" keys to the Amazonian *Pimelodus altipinnis* Steindachner, from which it is clearly different. Furthermore, Mees [1974] has identified the holotype of *altipinnis* as *Pimelodella cristata*. The names and relationships of these *Pimelodus*-like species are under study by D. J. Stewart.) Primitively in catfishes, and probably in most groups of fishes, the neural spines of the posterior precaudal and anterior caudal vertebrae angle at much less than 90° or curve posterodorsally from their centra.

8. Supraoccipital process: In *Exallodontus* the supraoccipital process (Fig. 6A) has a narrow and sharply-angular median ridge, below which the process sides have a slightly concave surface. Generally in catfishes, including pimelodids, that have a supraoc-

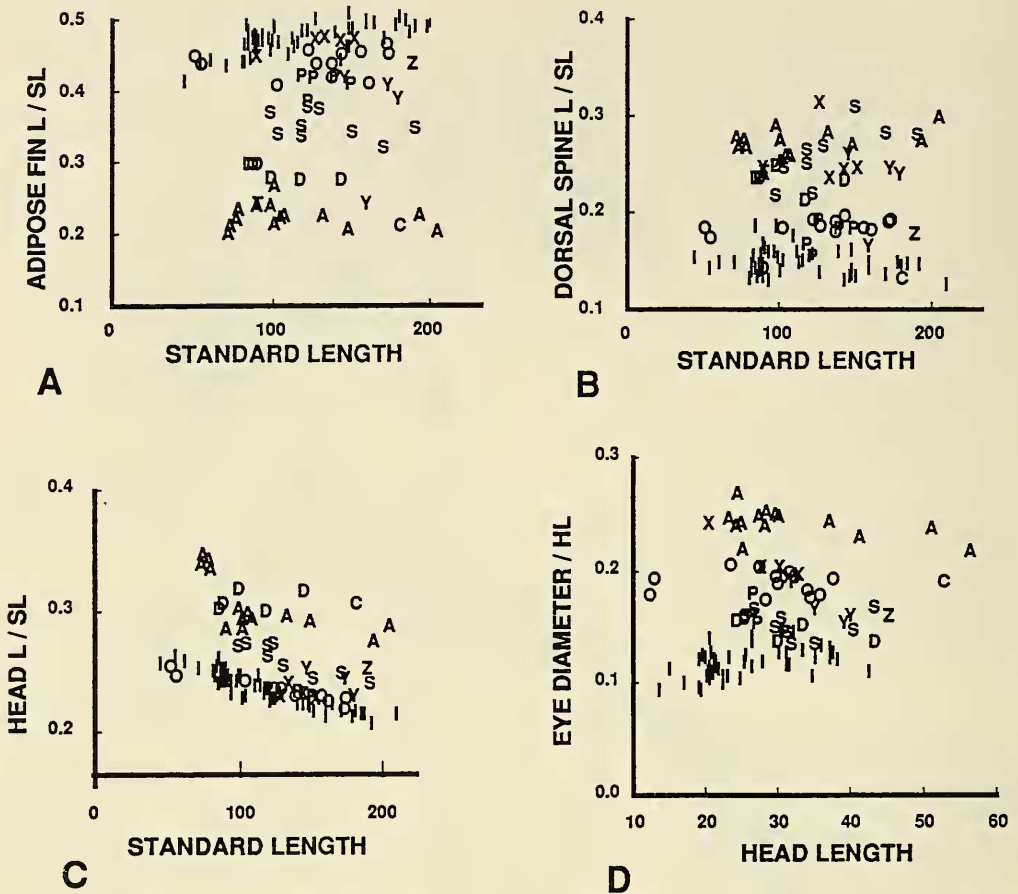


Fig. 5. Scatter plots of A. adipose fin length, B. dorsal spine length, C. head length, and D. eye diameter (expressed as ratios standard length or head length) for *Exallodontus aguanai* and similar pimelodine catfishes. Code to symbols: I = *E. aguanai*, A = *Pimelodus blochi*, C = *Duopalatinus emarginatus*, D = *Duopalatinus peruanus*, O = "Pimelodus A" from the Orinoco, P = "Pimelodus cf. A" from the Amazon, S = *Pimelodus altissimus*, X = *Pimelodina flavipinnis*, Y = *Calophysus macropterus*, Z = *Pinirampus pinirampu*.

cipital process, it is smoothly convex to flat. There are a few pimelodids, however, that have ridged supraoccipital processes: *Pimelodus altissimus* and *Duopalatinus peruanus*.

9. Anal-fin rays: Large specimens of *Exallodontus* have a paddle-like structure developed from thickened, elongated anterior fin rays. A similar but more hypertrophied structure is found in the undescribed species "Pimelodus A" from the Orinoco. Other pimelodids and most other catfishes lack such modified anal-fin rays.

10. Posterior nostril: Nearly all pimelo-

ids and other catfishes have an oval-shaped posterior nostril with its long axis oblique to the longitudinal body axis. *Exallodontus* similarly has an ovoid posterior nostril but its long axis is transverse (Fig. 7B). Among pimelodids a transverse orientation of the posterior nostril has been observed in *Leiaris*, *Calophysus*, *Pimelodina* and *Pinirampus*.

In the literature (Eigenmann & Allen 1942, Mees 1974) *Exallodontus* would be identified as a *Pimelodus*. However, three points justify description of *Exallodontus* as a new genus. First, this taxon is readily diagnosed

by uniquely autapomorphic features that mark it as a distinct lineage among the Pimelodidae. *Exallodontus* also has a unique combination of other features, some of which appear to be derived among pimelodids and eventually may be found to be additional autapomorphies of *Exallodontus* within a restricted subgroup of pimelodids, or synapomorphies shared with some other pimelodids. Second, because the sister group of *E. aguanai* is uncertain, we cannot assign this species to *Pimelodus* or another genus without risk of creating a nonmonophyletic group. Third, assignment of *E. aguanai* to *Pimelodus* would radically expand the limits of variation of an already vaguely diagnosed genus. Comparisons of *E. aguanai* and its phylogenetic position among pimelodids are discussed below.

Etymology.—*Exallodontus* from the Greek “exallos” for quite different, and “odontos” for tooth. This is in reference to the unique form of the teeth. The gender is masculine.

Exallodontus aguanai, new species

Figs. 2–10, 13, Tables 1–3

Holotype.—MBUCV-V-18930, 207.0 mm, Venezuela, Territorio Federal Delta Amacuro, Río Orinoco near Los Castillos, 159 n mi from sea buoy at the terminus of the ship navigation channel in Boca Grande, 8°32'N, 62°23'W, 10 Nov 1979, collected by R/V *Eastward* with a 9 m bottom trawl at a depth of 20–30 m.

Paratypes.—Venezuela: Apure State. ANSP 160185, 1, Río Meta upstream from confluence with Río Orinoco, ca. 6°18'N, 67°37'W, 27 Nov 1985, collected by B. Chernoff, W. Saul. MBUCV-V-15017, 1, 85.5 mm, Caño Bucaral, near mouth of Río Arauca, 7°20'N, 66°50'W, 9 Aug 1984, collected by O. Castillo, O. Brull, P. Nass. MBUCV-V-13072, 1, 165 mm, Río Apure in front of San Fernando de Apure, 7°55'N, 67°30'W, 14 Aug 1980, collected by O. Castillo, F. Provenzano. MBUCV-V-15381, 7,

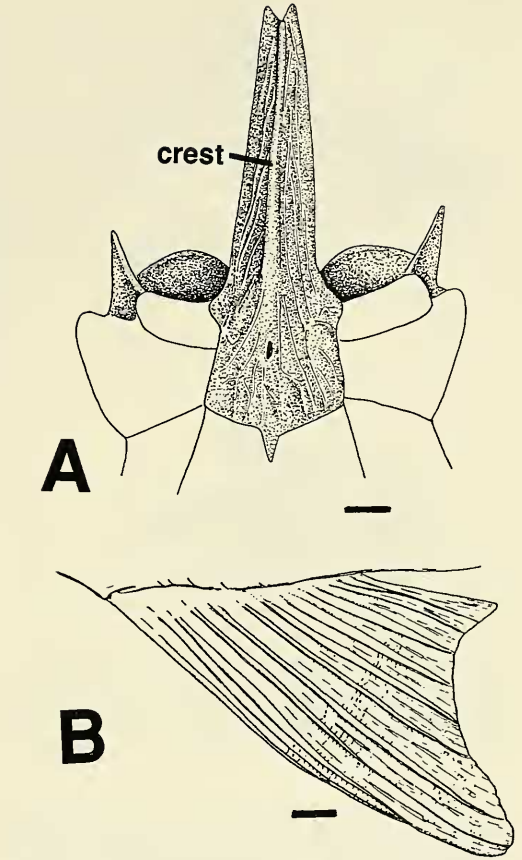


Fig. 6. A. Supraoccipital bone of *Exallodontus aguanai*, MBUCV-V-ES112. B. Anal fin, left side in lateral view, of *Exallodontus aguanai*, to show elongated anterior fin rays, Paratype ANSP 165813, mature specimen 149 mm SL from Río Orinoco, Venezuela. Scale bar for A = 2 mm, scale bar for B = 3 mm.

Río Apure at San Fernando de Apure, 7°55'N, 67°30'W. MBUCV-V-19055, 2, 32–123 mm, Río Apure in front of Laguna Jarina, near San Fernando de Apure, 7°55'N, 67°30'W, 21 May 1983, collected by F. Provenzano. MBUCV-V-19053, 2, 164–164 mm, Río Apure near mouth of Río Portuguesa, 7°55'N, 67°35'W, 22 May 1983, collected by F. Provenzano. MBUCV-V-19054, 2, 75–163 mm, Río Apure near mouth of Río Portuguesa, 7°55'N, 67°35'W, 27 Jul 1983, collected by F. Provenzano. MBUCV-V-19056, 3, 165–199 mm, Río Apure in front of Laguna Jarina, near San Fernando

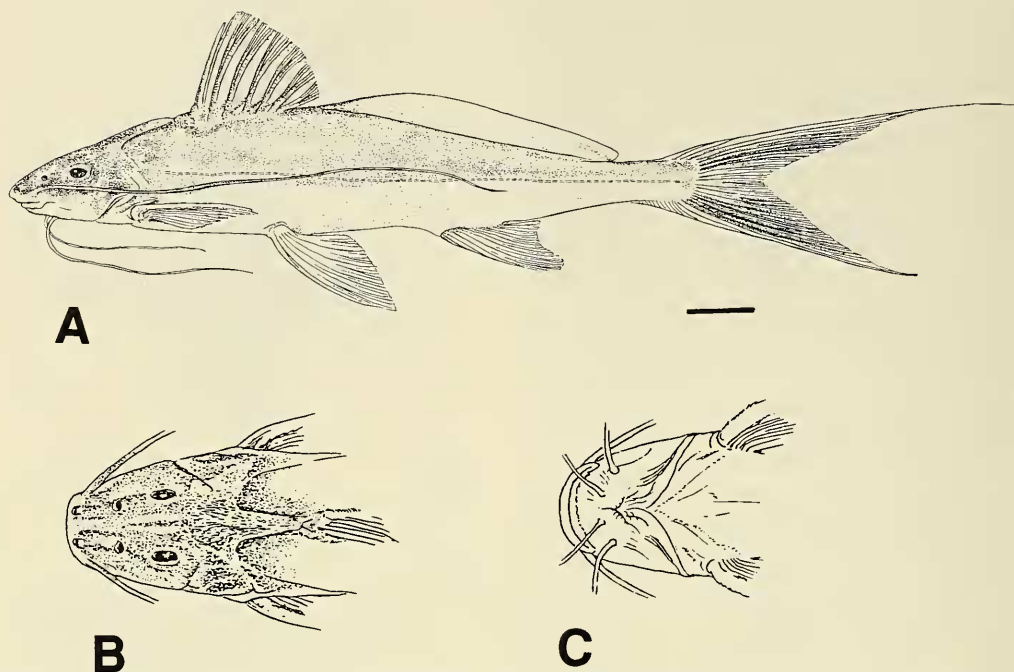


Fig. 7. *Exallodontus aguanai*, Paratype MBUCV-V-11012, mature specimen 175 mm SL from Río Orinoco, Venezuela, A. Left side lateral view, B and C. dorsal and ventral views of head. Single scale bar for A = 15 mm, for B, C = 20 mm.

de Apure, 7°55'N, 67°30'W, 18 Jun 1983, collected by F. Provenzano. MBUCV-V-19057, 4, 68–84 mm, Río Apure in front of airport at San Fernando de Apure, 7°55'N, 67°30'W, 12 Aug 1982, collected by F. Provenzano. MBUCV-V-19058, 5, 123–140 mm, Río Apure in front of Isla Apurito,

near San Fernando de Apure, 7°55'N, 67°30'W, 25 Jan 1985, collected by O. Castillo, F. Provenzano. Bolívar State (all collected by R/V *Eastward* in Río Orinoco). BMNH 1990.4.23:2–3, 2, 97–99 mm, 202 n mi from sea buoy, 8°18'N, 65° 56'W, 7 Nov 1979, field number T-9-79. CAS 63850,

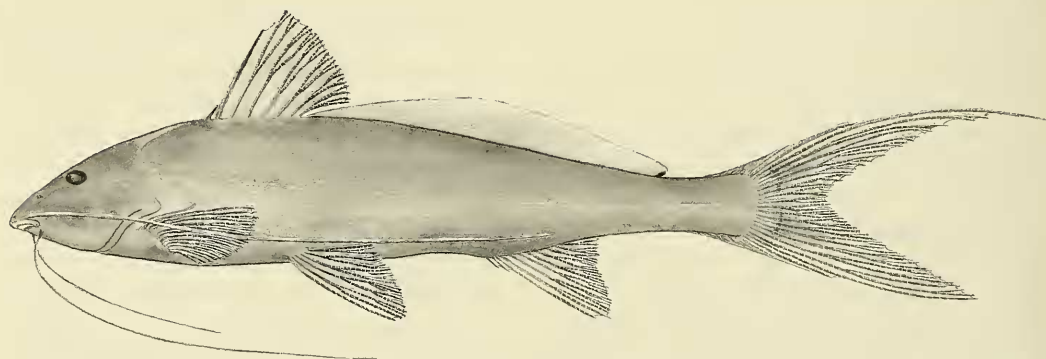


Fig. 8. *Exallodontus aguanai*, Paratype ANSP 15077, subadult from Peru, 91.5 mm SL. (Pectoral fin is unnaturally supinated.) Drawn by Ms. G. K. Jensen under the direction of Dr. J. Böhlke.

2, 100–128 mm, 203 n mi from sea buoy, 8°21'N, 62°57'W, 7 Nov 1979, Field number T-11-79. Territorio Federal Delta Amacuro (all collected by R/V *Eastward* in Río Orinoco). AMNH 59041, 3, 113–118 mm, near Los Castillos, 160 n mi from sea buoy, 8°32'N, 62°24'W, 10 Nov 1979, field number T-23-79. ANSP 165812, 5, 89–123 mm, near mouth of Caño Tortola, 137 n mi from sea buoy, 8°42'N, 62°05'W, 12 Nov 1979, collected by R/V *Eastward*, field number T-43-79. ANSP 165813, 2, 149–180 mm, 2 km below Barrancas, 140 n mi from sea buoy, 8°44'N, 62°07'W, 17 Feb 1978, collected by R/V *Eastward*, field number JGL-16-78. ANSP 165814, 1, 158 mm, near Isla Veradero downstream from Barrancas, 141 n mi from sea buoy, 8°43'N, 62°08'W, 17 Feb 1978, field number JNB-26-78. DU-F-977, 4, incl. a dry skeleton, 159–180 mm, upstream from El Consejo, 135 n mi from sea buoy, 8°42'N, 62°04'W, 19 Feb 1978, field number JNB-44-78. DU-F-865, 5, incl. 1 cleared and stained, 82–94 mm, near mouth of Caño Tortola, 137 n mi from sea buoy, 8°42'N, 62°05'W, 12 Nov 1979, field number T-45-79. FMNH 99441, 4, 92–111 mm, near mouth of Caño Guine, downstream from El Consejo, 133 n mi from sea buoy, 8°40'N, 62°02'W, 13 Nov 1979, field number T-50-79. FMNH 99442, 3, 119–163 mm, near Barrancas, 141 n mi from sea buoy, 8°42'N, 62°10'W, 12 Nov 1979, field number T-39-79. MBUCV-V-11012, 2, 156–175 mm, near El Consejo, about 136 n mi from sea buoy, 8°42'N, 62°05'W, 19 Feb 1978. MBUCV-V-13734, 1, 190 mm, Isla Portuguesa, 16 Nov 1979. MZUSP 41395, 1, 118 mm, downstream from El Consejo, 130 n mi from sea buoy, 8°40'N, 62°00'W, 14 Nov 1979, field number T-56-79. UMMZ 217309, 2, 78–119 mm, near Caño Araguaito, 130 n mi from sea buoy, 8°40'N, 61°59'W, 22 Nov 1979, field number HLR-42-79. USNM 308421, 1, 188 mm, N side of Isla Tres Caños near mouth of Caño Araguaito, 130 n mi from sea buoy, 8°40'N, 61°59'W, 19 Feb 1978, field num-

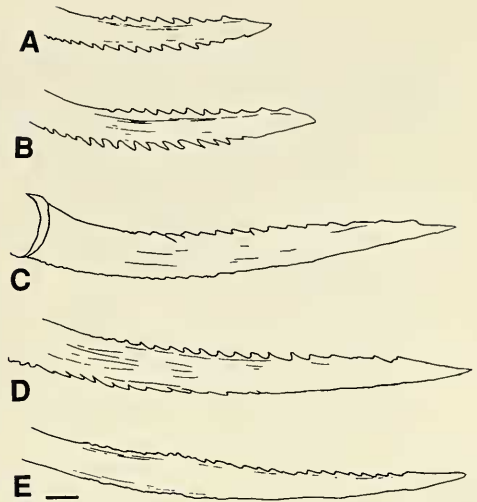


Fig. 9. Dorsal views of left pectoral spines of *Exallodontus aguanai* illustrating negative allometry of dentations. A. Venezuelan specimen 46.9 mm SL, MBUCV-V-19059, B. Peruvian specimen 59.5 mm SL, ANSP 150178, C. Venezuelan specimen 82.5 mm SL, DU-F-1048, D. Peruvian specimen 91.5 mm SL, ANSP 150177, E. Venezuelan specimen, 199.4 mm SL, MBUCV-V-11012. Single scale bar for A and D = 1 mm; for E = 2 mm.

ber JNB-37-78. USNM 308422, 1, 93 mm, near Los Castillos, 161 n mi from sea buoy, 8°31'N, 62°25'W, 10 Nov 1979, field number T-22-79. USNM 308423, 7, 74–115 mm, near mouth of Caño Guine downstream from El Consejo, 133 n mi from sea buoy, 8°40'N 62°02'W, 13 Nov 1979, field number T-54-79. USNM 320097, 1, 124 mm, near Puerto Cabrian, 151 n mi from sea buoy, 8°35'N, 62°16'W, 11 Nov 1979, field number T-35-79. Monagas State (all collected by R/V *Eastward* in Río Orinoco). LACM 43311-1, 2, 85–111 mm, near Caño los Cocos, across from Los Castillos, 162 n mi from sea buoy, 8°32'N, 62°25'W, 10 Nov 1979, field number HLR-13-79. MBUCV-V-10661, 1, 127 mm, near Barrancas, between N coast and Isla Veradero, ca. 141 n mile from sea buoy, 8°42'N, 62°10'W, 17 Feb 1978. MBUCV-V-13961, 1, 177 mm, collected near Barrancas, between N coast and Isla Veradero, ca. 141 n mile from sea buoy, 8°42'N, 62°10'W, 17 Feb 1978.



Fig. 10. Geographic distribution of *Exallodotus aguanai* in the Orinoco and Amazon basins. Star = type locality; some symbols represent more than one lot of specimens, see text under Distribution.

Peru: Loreto Department. ANSP 150177, 91.5 mm, and ANSP 150178, 59.5 mm, both from vicinity of Iquitos, Río Amazonas (Marañón) between Isla Iquitos and Isla Lapuna, near Isla Lapuna shore; to 3.66 m in trawl net, 3°51'S, 73°13'W, 9 Oct 1955, collected by C. C. G. Chaplin and R. Patrick.

Brazil: Amazonas. INPA 4450, 1, 140 mm, Río Amazonas 2–3 km downstream of Manaus, collected with 3 m try net trawl in channels ca. 20–40 m, 3°40'S, 59°40'W, Nov 1990, collected by J. Lundberg, L. Py-Daniel, N. L. Chao, and C. Cox Fernandes. INPA 4451, 2, 47–64 mm, Río Solimões, 5 km upstream of Manaus with 3 m try net trawl in channels ca. 20–40 m, 3°10'S, 60°20'W, Dec 1990, collected by J. Lundberg, L. Py-Daniel, N. L. Chao, and C. Cox Fernandes.

Non-type specimens examined.—Venezuela: Apure State. MBUCV-V-19059, 4 cleared and stained, 48–61 mm, Río Apure in front of Boquerones near San Fernando de Apure, 7°55'N, 67°30'W, collected by F. Provenzano. Bolívar State (all collected by R/V *Eastward* in Río Orinoco). DU-F-1024, 1, 145 mm, near Ciudad Bolívar, 241 n mi from sea buoy, 8°09'N, 63°32'W, 9 Nov 1979, field number ECM-2-79. DU-F-1025,

1, 88 mm, near San Felix S of Isla Fajardo, 180 n mi from sea buoy, 8°22'N, 62°40'W, 6 Nov 1979, field number T-1-79. DU-F-1026, 1, 90 mm, 202 n mi from sea buoy, 8°18'N, 65°56'W, 7 Nov 1979, field number T-10-79. DU-F-1027, 1, 90 mm, 201 n mi from sea buoy, 8°18'N, 62°56'W, 8 Nov

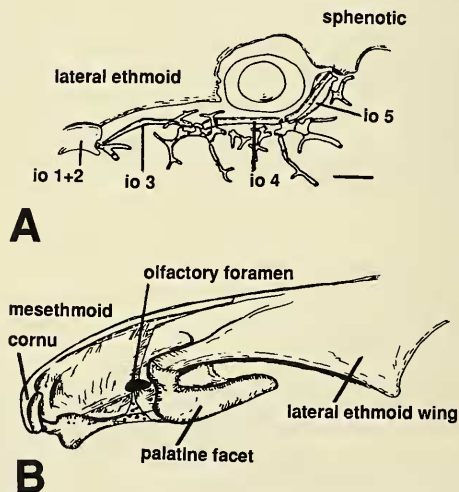


Fig. 11. A. Dendritic arrangement of lateral line tubes as exemplified by infraorbital region of *Pimelodus altissimus*, AMNH 40138. B. Elongated palatine facet on the lateral ethmoid as exemplified by *Pimelodus grosskopfii*, DU-F-919. Single scale bar for both = 2 mm.

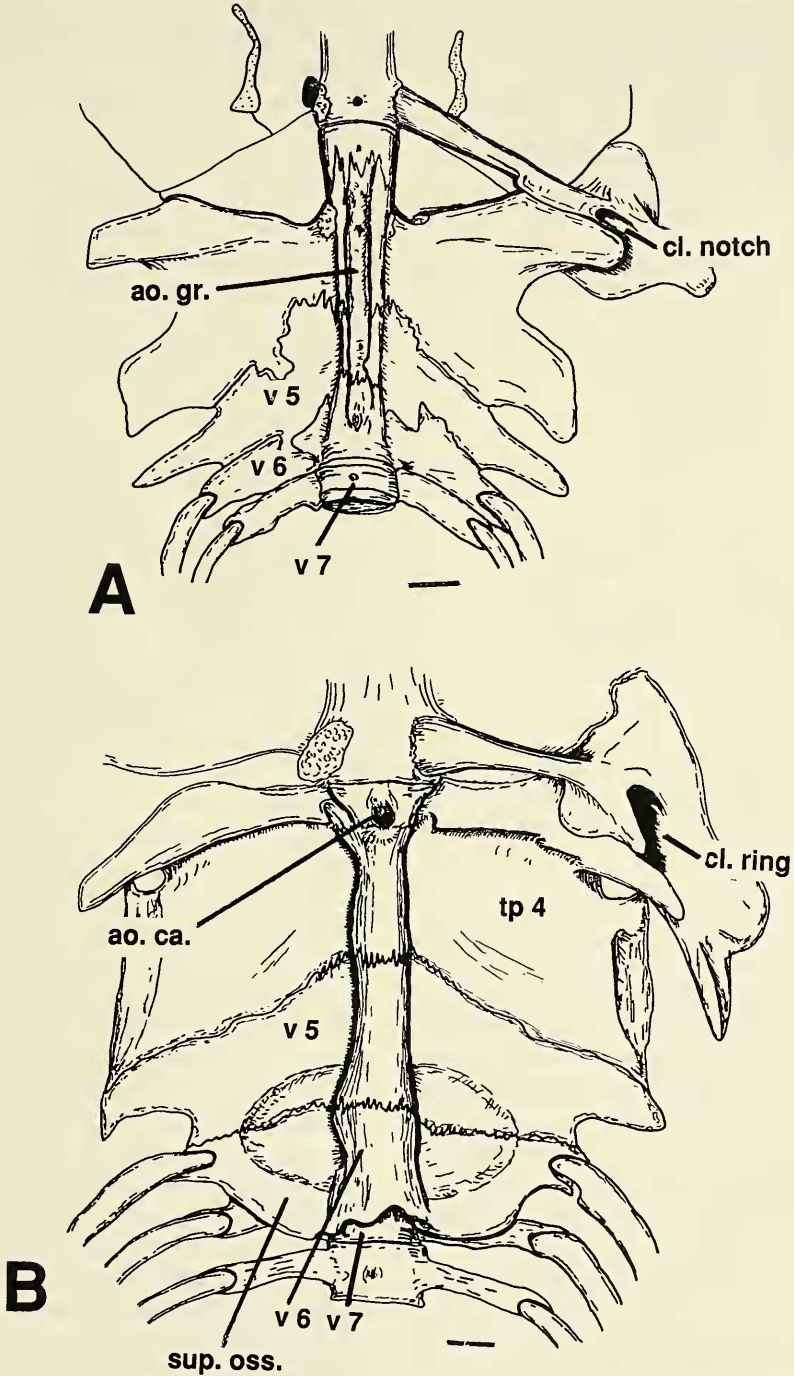


Fig. 12. Weberian complex, basioccipital region and upper part of shoulder girdle of A. *Phractocephalus hemiliopterus*, DU-F-925, and B. *Pimelodus grosskopfii*, DU-F-919, Scale bar for A = 5 mm, for B = 2 mm. ao. ca. = aortic canal; ao. gr. = aortic groove; cl. notch = notch for cleithrum in supracleithrum; cl. ring = "cleithral ring"; sup. oss. = superficial ossification on vertebral centra; tp4 = transverse process of vertebra 4; V5, V6, V7 = vertebrae with their ordinal numbers.

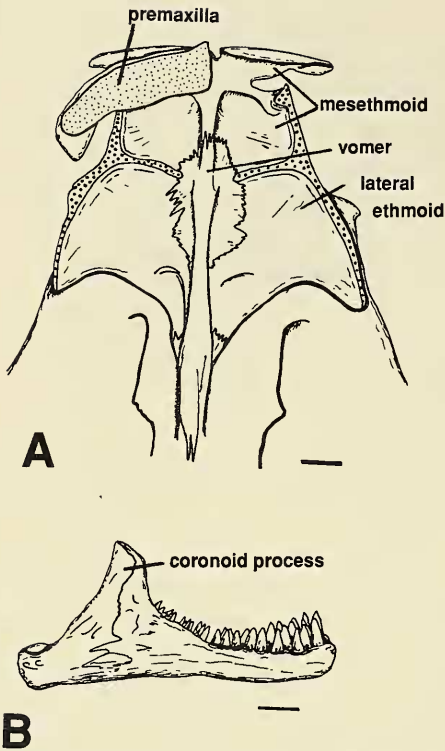


Fig. 13. A. Ethmoid region in ventral view of *Pimelodus grosskopfii*, DU-F-919, B. Right mandible of *Exallodontus aguanaei*, DU-F-977, Single scale bar for both = 2 mm.

1979, field number T-13-79. DU-F-1028, 1, 90 mm, near Puerto Ordaz, N of Isla Fajardo, 180 n mi from sea buoy, 8°24'N, 62°40'W, 23 Nov 1979, field number T-84-79. Territorio Federal Delta Amacuro (all collected by R/V *Eastward* in Río Orinoco). DU-F-1029, 1, 136 mm, near Barrancas, 139 n mi from sea buoy, 8°44'N, 62°07'W, 17 Feb 1978, field number JGL-19-78. DU-F-1030, 4, 159-180 mm, S of Isla Portuguesa, 117 n mi from sea buoy, 8°36'N, 61°48'W, 20 Feb 1978, field number JGL-44-78. DU-F-1031, 1, 86 mm, near Los Castillos, 161 n mi from sea buoy, 8°31'N, 62°24'W, 10 Nov 1979, field number T-20-79. DU-F-1032, 1, 95 mm, near Los Castillos, 160 n mi from sea buoy, 8°32'N, 62°23'W, 10 Nov 1979, field number T-27-79. DU-F-1033, 1, 107 mm, downstream

from Isla Portuguesa, 116 n mi from sea buoy, 8°36'N, 61°47'W, 14 Nov 1979, field number T-60-79.

Diagnosis.—The same as that of the genus.

Description.—Lateral, dorsal and ventral views in Figs. 7 and 8 illustrate head and body shape, form and position of fins, and pigment pattern. Variational data for morphometric and meristic characters are given in Tables 1–3. Additional features are described and compared in the section on phylogenetic relationships.

Cranial roof partly visible through thin and transparent integument; bones near midline coarsely sculptured with anastomosing, longitudinally-trending ridges; sphenotic and temporal region bones sculptured with irregularly oriented ridges (cranial bone texture not to be confused with overlying dendritic sensory canal branches, see below). Anterior cranial fontanelle open from level of posterior nares to posterior margin of orbit, followed posteriorly by a shallow groove to level of pterotic; fontanelle and groove covered above with pale integument. Posterior cranial fontanelle a small or minute foramen at base of supraoccipital process (Fig. 6A).

Mouth distinctly subterminal; snout projecting beyond upper lip by a distance about equal to horizontal diameter of eye. Mouth opening anteroventrally; margin of closed mouth smoothly curved; one or two rows of premaxillary teeth exposed; corner of closed mouth a little anterior to a vertical from anterior edge of posterior naris; gape width about equal to distance across lower margins of orbital rims. Upper lip smooth or with a few coarse papillae immediately adjacent to premaxillary teeth; the lower lip weakly plicate; both lips without accessory folds paralleling tooth rows. Fleishy rictal fold in a pocket behind corner of mouth, scarcely protruding above general surface of head; a shallow groove extends anterodorsally from rictal fold to terminate anterior to base of maxillary barbel; ventral to rictal

Table 1.—Standard lengths and proportionate characters for *Exallodontus aguanai* expressed in thousandths of the standard dimensions given in parentheses (SL—standard length, CPL—caudal peduncle length, ADL—adipose fin length, AFB—anal fin base, HL—head length); means for Orinoco sample followed by ranges in brackets, and sample size.

Measurement	Orinoco sample	Holotype MBUCV 18930	Amazon sample		
			ANSP 150177	ANSP 150178	INPA 4550
Standard length (mm)	115.4 [43.5–207.0] 52	207.0	91.9	59.5	140.0
Predorsal fin length (SL)	310 [283–342] 52	292	331	304	296
Prepectoral fin length (SL)	203 [174–257] 32	179	220	190	204
Preanal fin length (SL)	643 [615–671] 32	651	659	640	640
Head length (SL)	225 [191–253] 52	204	247	220	214
Caudal peduncle length (SL)	257 [227–279] 52	265	252	245	261
Caudal peduncle depth (CPL)	292 [263–338] 32	290	293	284	287
Adipose fin length (SL)	463 [402–498] 52	479	469	431	472
Adipose fin height (ADL)	137 [104–206] 32	113	163	116	144
Anal fin base (SL)	92 [76–104] 20	85	96	—	109
Anal fin height (AFB)	2058 [1798–2387] 20	2080	2000	—	1907
Pelvic fin length (SL)	210 [183–243] 52	195	219	208	212
Urogenital papilla-anal fin (SL)	190 [132–238] 38	190	180	142	209
Pectoral spine length (SL)	157 [139–180] 48	158	158	153	170
Dorsal spine length (SL)	140 [116–178] 48	116	140	122	138
Dorsal fin base (SL)	143 [134–160] 18	137	133	131	140
Dorsal fin height (SL)	170 [146–190] 31	161	163	163	186
Body depth (SL)	202 [171–242] 52	215	197	182	211
Body width (SL)	173 [155–190] 52	170	165	184	169
Posterior cleithral process (SL)	88 [77–97] 32	85	92	88	79
Bony interorbital (HL)	258 [229–286] 32	258	293	267	264
Interocular (HL)	319 [294–350] 37	334	333	307	301
Eye diameter (HL)	108 [83–135] 51	100	128	102	90
Snout length (HL)	466 [433–514] 52	488	465	456	458
Internarial length (HL)	217 [181–246] 38	199	213	211	194
Internarial width (HL)	183 [172–194] 18	180	183	183	167

fold a thin submandibular groove extends about $\frac{1}{2}$ distance to symphysis. Jaw teeth (Fig. 2) described in diagnosis of genus; no teeth on palate. Upper oral valve broader and longer than premaxillary tooth bands; with a small, raised epithelial patch on the midline (scanning electron microscope observations made on similar median structures in several other catfishes reveal the presence of many taste buds).

Barbels thin, proximally flattened but lacking membranous edges. Maxillary barbel reaching to beyond origin of anal fin; inserted midway between anterior nostril and posterior end of rictal fold. Mental barbels inserted in advance of gular fold apex, in a curved line parallel to lower jaw margin.

Inner mental barbels 1.5–2 times closer to gular fold than to margin of lower jaw; inner mental barbels reach to about 0.5 length of depressed pectoral fin. Outer mental barbels reach to 0.5 length or more of depressed pelvic fin. Gular fold overlying a deep groove, its sides meeting in an obtuse angle; each side equal to or a little greater than distance between inner and outer mental barbels. Gill membranes free, diverging at once from gular fold apex, supported by 8 branchiostegal rays (1 on posterior ceratohyal + 1 on cartilage between ceratohyals + 6 on anterior ceratohyal). Gill rakers on first branchial arch 19–21 (5–6 on upper limb, 1 at angle, 13–14 on lower limb, $n = 4$). Upper and lower pharyngeal teeth robust

Table 2.—Frequency distribution of anal-fin ray counts in *Exallodontus aguanai*.

Total rays	11			12			13			14		
Formulae	iv7	v7	iv8	vi7	v8	iv9	v9	iv10				
Venezuela (<i>n</i> = 19)	4	1	6	1	3	2	1					
Amazon (<i>n</i> = 5)						1	2	2				

with straight to scarcely recurved crowns. Anterior nostril located dorsally on snout, behind snout tip by about its own diameter and a little anterior to a line between anterior edges of maxillary barbel bases; its rim tubular and flaring; its aperture about 0.3 of orbital diameter. Posterior nostril medially offset from a line between anterior border of orbit and anterior nostril; its rim a thin membrane elevated anteriorly and curving $\frac{2}{3}$ distance around aperture, incomplete posteriorly; its aperture ovoid with transverse principal axis. Eye small, centered on midlength of head and about 45° above mid-frontal plane. Orbital rim fleshy and free. Orbital opening ovoid, its vertical diameter contained 1.3–2 times in horizontal diameter; visible part of eye comprising mostly pupil and lens.

Head lateralis system with superficial, many-branched tubes that lead to minute pores on nape, top of head, cheeks, operculum and mandible. (The complex dendritic structure of the lateralis system precludes external enumeration and comparison of the primary branches that exit through dermal bone foramina. This subject is under study as part of a broader investigation of pimelodid systematics.) Lateral line canal complete, reaching onto base of middle caudal rays, curved slightly ventrad

over hypurals; its anterior tubes dendritic over lateral cutaneous area; tubular ossicles surround lateral line to below dorsal-fin base, these not visible externally.

Dorsal fin with eight rays: a spinelet, a strong and pungent spine, and 6 soft rays; bases of last two rays separate; distal margin gently convex; length of last ray a little less than half that of first. Spinelet (ray 1) with a narrow median crest recalling crest on supraoccipital process. Dorsal spine with a compressed, anterior median ridge, sharply elevated proximally where it is ligamentously tied to spinelet. Dorsal spine (ray 2) with a few small retrorse dentations posterodistally. Adipose fin long, high, straight-margined for most of its length, ending in a short free lobe; its origin close to dorsal fin; its highest point anterior to anal-fin origin. Caudal fin deeply forked, its lobes with concave inner margins; upper lobe produced, its outer principal ray filamentous; shortest middle caudal rays contained in longest upper rays 4–5 times, and about 3 times in longest lower rays; principal caudal rays 1, 7–8, 1; procurrent caudal rays 12–15 upper, 10–18 lower. Anal fin (Fig. 6B) with a concave distal margin; anal-fin rays 11–14, the first 4–6 rays simple (Table 2), anterior 3 branched rays and longest simple ray produced to form a blunt paddle-like

Table 3.—Frequency distribution of vertebral counts in *Exallodontus aguanai*. Precaudal vs. caudal distinction indeterminate in one dry skeleton from Venezuela.

Classes	Precaudal			Caudal					Total		
	16	17	18	29	30	31	32	33	46	47	50
Venezuela (<i>n</i> = 5)	3	1		1	1	2			2	3	
Amazon (<i>n</i> = 2)		1	1				1	1			2

projection in largest specimens (of six dissected all are female); fin rays of paddle exceeding tip of last anal ray but not reaching below end of adipose fin.

Pectoral fin with a spine plus 10–11 soft branched rays; its distal margin truncate except first soft ray a little longer than spine tip; depressed pectoral fin reaches to below fourth–fifth dorsal-fin soft rays and short of a vertical at pelvic-fin origin. Pectoral spine (Fig. 9) strong, sharp; no or weak anterior distal serrae, but with antrorse to erect anterior dentations along proximal $\frac{3}{4}$, and retrorse dentations present along most of posterior margin. Anterior dentations very strongly developed in small specimens, becoming progressively less prominent and more crowded basally. Posterior dentations unicuspid and mostly regularly spaced. Posterior cleithral process deep and acutely triangular with a sharply pointed tip; its surface ornamented with fine osseous ridges and a few weakly developed tubercles. No axillary-pore below postcleithral process. Pelvic fin with 6 soft rays, the first simple. Pelvic-fin origin below penultimate dorsal-fin ray; its distal margin truncate, except first branched ray a little longer than first, pelvic-fin length contained in SL 4.1–5.5 times; distance between tip of depressed pelvic fin and anal-fin origin about equal to anal-fin base length.

Total vertebrae 46–50, 16–18 precaudals and 29–33 caudals (Table 3).

Urogenital papilla with no apparent sexual dimorphism; located in a shallow depression immediately behind anus and between pelvic fins about midway along length of their inner fin rays.

Color in alcohol.—Most specimens preserved in alcohol are countershaded with an abrupt demarcation at lateral line. Dorsal to the lateral line, sides and fleshy part of nape are dark to light grayish-purple or grayish-tan; cheeks and sides of snout similarly colored. Sides ventral to lateral line, venter of body, head and snout tip much lighter, often white. Dorsum of head dull

yellow (imparted by underlying bones) and finely streaked with irregular lines of dark chromatophores. Narial region flanked medially by short dark stripe dorsal to nasal bone, and usually by a short dark stripe dorsal to “lacrimal.” Barbels dusky dorsally, white ventrally. Fins hyaline distally, but interradiation membranes pale white to yellowish proximally. Some specimens have dark lines on anterior margins of dorsal-fin rays. In most specimens each caudal-fin lobe has a dark medial stripe tapering caudad from an obscure basal blotch over middle 3 or 4 rays.

Color upon capture.—Specimens from both the Orinoco and Amazon have a metallic green to brassy sheen on nape to either side of supraoccipital process, sides dorsal to pectoral fin, sides and venter of head. Dorsum of head over skull bones dark gray to black. Flanks, venter, adipose fin base, barbels, pectoral and dorsal spines white. All fins dull yellow-orange, and each caudal-fin lobe has a longitudinal dark gray to black stripe over middle 3 or 4 rays.

Distribution and ecology.—*Exallodontus* presently is known to occur in Venezuela in the mainstem of the lower Río Orinoco and in middle Orinoco basin in the Apure and Meta rivers, and in the Amazon mainstem near Iquitos, Peru and Manaus, Brazil (Fig. 10). All specimens have been taken by bottom trawls in the main channels of large rivers at depths ranging from about 3–35 m, in current speeds exceeding 1.5 m/sec, and on sandy to detritus-covered substrates. We expect that further collecting with trawls in large rivers of the Amazon and Orinoco systems will reveal a wider distribution of this species. *Exallodontus aguanai* is commonly associated with other catfishes (pimelodids, doradids, cetopsids, loricariids), electric fishes (sternopygids, apteronotids, rhamphichthyids, hypopomids) and freshwater sciaenids (López et al. 1985).

Variation.—Despite the large distance between the Orinoco and Amazon samples of *E. aguanai*, there is no apparent differ-

entiation. The two Peruvian specimens have 50 vertebrae in contrast to 46–47 in the Orinoco subsample (Table 3). However, a total intraspecific range of variation of five vertebrae is not unexpectedly high for catfishes.

Etymology.—The specific name, *aguanaei*, honors Sr. Leonidas Aguana of the Instituto de Zoología Tropical, Universidad Central de Venezuela, whose long friendship with the authors and intrepid collaboration in the field have contributed greatly to this research and to Venezuelan ichthyology.

Relationships.—This section begins with a delimitation and phylogenetic diagnosis of the subfamily Pimelodinae to which *Exallodontus* belongs. We then review a nested set of synapomorphies, in descending hierarchical order, that relate *Exallodontus* to subgroups of pimelodines. Inference of character polarities is based on the outgroup framework outlined above in Methods, and the outgroup taxa and specimens are listed below under comparative materials. Although we are unable to completely resolve the sister group relationship of *Exallodontus*, we have discovered sufficient evidence to develop a hypothesis on its proximate relatives. The results of this phylogenetic analysis are summarized in Fig. 1. Except for the subfamily Pimelodinae, we use informal names to refer to various generic groups. We believe that formal naming and diagnosing of these subgroups would be premature in light of ongoing research and manuscripts in preparation by us and Donald J. Stewart.

Subfamily Pimelodinae

Membership.—Based on examination of available specimens (those represented by skeletal specimens marked by *) or literature descriptions, we assign the following nominal genera to the Pimelodinae (see also Fig. 1): *Aguarunichthys*, *Bagropsis*, *Bergia*, *Brachyplatystoma**, *Calophysus**, *Cheirocerus**, *Conorhynchus*, *Duopalati-*

*nus**, *Exallodontus**, *Goslinia**, *Hemisorubim**, *Hypophthalmus**, *Iheringichthys**, *Leiarius**, *Luciopimelodus*, *Megalonema**, *Merodontodus*, *Perrunichthys*, *Parapimelodus**, *Paulicea**, *Phractocephalus**, *Pimelodina**, *Pimelodus**, *Pinirampus**, *Piranutana*, *Platynemachthys**, *Platysilurus**, *Platystomachthys**, *Pseudoplatystoma**, *Sorubim**, *Sorubimichthys**, and *Steindachneridion**.

Diagnosis.—Three synapomorphic characters support the group of nominal genera here united as the Pimelodinae. For additional description and illustrations of these characteristics see Lundberg & McDade (1986), Lundberg et al. (1988), and Lundberg et al. (1991).

(1) Dendritic arrangement of lateral line tubes in skin of snout, cheek and nape (Fig. 11A). Other pimelodids and most other catfishes, including diplomystids, have simple unbranched lateralis tubes.

(2) Uniquely shaped, much elongated articulation surface on lateral ethmoid for palatine (Fig. 11B). Plesiomorphically this joint surface has the form of a foreshortened, inverted triangle as is found in other pimelodids and other outgroup catfishes, including diplomystids and †*Hypsidoris*.

(3) Deep sutural joint between fifth and sixth centra (Fig. 12A & B). In other pimelodids and most other catfishes, including diplomystids and †*Hypsidoris*, there is a typical intervertebral joint between the fifth and sixth centra. *Megalonema*, which we place in the Pimelodinae, is exceptional in having a normal, non-sutural joint between vertebrae five and six (Stewart 1986a). Howes 1983:37, reported for *Megalonema* "the 5th and 6th centra fused within the vertebral complex," based on a dissected specimen; our observations concur with Stewart's and are made on cleared and stained specimens. We interpret this as a reversal in *Megalonema*, not a primitive characteristic, because *Megalonema* possess the nested synapomorphies for three subgroups within the subfamily as outlined

below: "Group A," the "*Calophysus-Pimelodus* clade," and, in part, the "*Calophysus* group."

Lundberg et al. (1988) listed another putative synapomorphy for the clade here referred to as Pimelodinae: a bony canal, for an asymmetrically enlarged postcardinal vein, on the ventral surface, left side, of the Weberian complex at the angle between the centra and transverse processes. We have since observed that this feature occurs more broadly among pimelodids and in some other catfish families (e.g., Siluridae, Bornbusch 1988). Among pimelodids the asymmetry of veins and left side bony canal are present in *Pseudopimelodus apurensis* and *Zungaro zungaro*. Based on other evidence, these two species belong to the monophyletic subfamily Pseudopimelodinae that also includes the nominal genera *Lophiosilurus* and *Microglanis* (Lundberg et al. 1988, Lundberg et al. 1991). Available representatives of the last two genera lack the venous and skeletal asymmetry. All other pimelodids examined, in particular the Rhamdiinae (Lundberg et al. 1991, = Group B of Lundberg et al. 1988), have symmetrical postcardinal veins and lack bony canals. Consequently, the derived asymmetrical condition of the postcardinal veins is incongruent with current hypotheses of relationships. It remains to be determined if the asymmetrical structures are relevant to more inclusive taxonomic levels than suggested by Lundberg et al. (1988).

Subfamily name.—The Pimelodinae takes its name from *Pimelodus* Lacépède (1803), the oldest-named member genus. Günther (1864) employed the name Pimelodina (not the genus) for an assemblage nearly equivalent to the Pimelodidae of modern authors. The subfamily name Pimelodinae has been applied to more or less the same group. Eigenmann & Eigenmann (1890) first used Pimelodinae for a subfamily within the Siluridae, then an ample family that included most catfishes (Bleeker 1862, Günther 1864, Gill 1872). Eigenmann & Eigenmann's Pime-

lodinae excluded *Calophysus*, which they placed in its own subfamily, and included genera that are now placed in other subfamilies (Rhamdiinae and Pseudopimelodinae). With the acceptance of Regan's (1911) catfish families, the Pimelodinae became a subfamily within the Pimelodidae. While various relatively apomorphic pimelodid genera were set off in their own subfamilies, the Pimelodinae has remained a large, poorly defined and catch-all group. Thus, Driver (1919) established the Luciopimelodinae for *Luciopimelodus* and *Megalonema* (Driver also included *Perugia* which has been shown to be a synonym of *Pinirampus* by Stewart 1986a). Schultz (1944) united in the Sorubiminae the nominal genera *Brachyplatystoma*, *Duopalatinus*, *Hemisorubim*, *Leiaris*, *Perrunichthys*, *Paulicea*, *Phractocephalus*, *Platynemachthys*, *Platysilurus*, *Platystomachthys*, *Pseudoplatystoma*, *Sorubim*, *Sorubimichthys*, and *Steindachneridion*. Also, apparently based on shared absence of certain obvious specializations, the auchenipterid catfishes were included in the Pimelodinae by Eigenmann & Allen (1942), but their classification position has never been followed.

"Group A."—Within the taxon here named Pimelodinae, Lundberg et al. (1988) proposed an informally-named "Group A" that is the sister group to a small clade comprising *Phractocephalus*, *Leiaris* and *Perrunichthys* (Fig. 1). *Exallodontus* belongs to "Group A."

In support of "Group A" Lundberg et al. (1988), following the lead of Howes (1983), listed one synapomorphic feature: osseous "aortic tunnel" or canal on ventral side of Weberian centra (Fig. 12B ao. ca.). The aortic canal, containing the dorsal aorta, is formed by extension of the superficial ossification over the midventral aortic groove usually from centrum 1 to 5 or 6 (but restricted to the compound Weberian centrum in *Megalonema*). Other pimelodids and most other catfishes, including diplo-mystids and †thypsidorids, have an open

midventral aortic groove on these centra (Fig. 12A ao. gr.). A more extensive type of aortic tunnel running from the basioccipital to beyond the sixth vertebra is found in the Ariidae, and small bridges of bone span the aortic groove in some doradids and *Age-neiosus*.

Calophysus-Pimelodus clade.—Four putative synapomorphies lead to a hypothesis of monophyly of a large group of genera within “Group A” comprising the “*Calophysus* group” (Stewart 1986a), *Megalonema*, and our “*Pimelodus* group” (see below and Fig. 1). Stewart (1986a) presented evidence for monophyly of a “*Calophysus* group” including the genera *Calophysus*, *Pinirampus*, *Pimelodina*, *Luciopimelodus* and *Aguarunichthys*. Stewart excluded *Megalonema* from the “*Calophysus* group,” but noted that these taxa share derived characteristics of the slender pectoral spine, high pectoral fin-ray count, and loss of the posterior cleithral process. We tentatively place *Megalonema* as the sister taxon to the “*Calophysus* group.” Howes (1983) suggested that *Hypophthalmus*, usually isolated in its own family, may be closely related to a group of pimelodids including some members of our “*Calophysus-Pimelodus* clade.” In agreement with Howes, we classify *Hypophthalmus* among the Pimelodidae (and Pimelodinae). However, *Hypophthalmus* does not share the synapomorphies that support the “*Calophysus-Pimelodus* clade” and we consider its position to be indeterminate within the subfamily. *Exallodontus* is a member of the “*Calophysus-Pimelodus* clade.” The four synapomorphies of this lineage follow.

(1) Ossified posterior part of ethmoid plate, i.e., posteroventral part of mesethmoid, has parallel sides, and abruptly-rounded, to nearly right-angled, corners (Fig. 13A; see also fig. 5B of *Pimelodus pictus*, Lundberg & McDade 1986; and fig. 1c of *Pimelodina flavipinnis*, Stewart 1986a). Also, because the vomer lacks prominent

lateral processes, the synchondral (sometimes sutural) joint between the mesethmoid and lateral ethmoid is widely exposed. In its plesiomorphic form, found in pseudopimelodines (Lundberg et al. 1991), other pimelodines, and most other catfishes including diplomystids and †hypsidorids, the ethmoid plate has concave sides and acutely-angled posterolateral corners. Lundberg & McDade (1986), Ferraris (1988) and Lundberg et al. (1991) described another uniquely and separately derived form of the lateral synchondral joint between the mesethmoid and lateral ethmoid that characterizes the subfamily Rhamdiinae.

(2) Mesethmoid cornua abruptly deflected ventrad and with a small or no median cleft (Fig. 13A; see also Lundberg & McDade 1985: fig. 5B, Stewart & Pavlik 1985: fig. 2; Stewart 1986a: fig. 1c). In other pimelodids and catfishes that have mesethmoid cornua, including diplomystids and †hypsidorids, these structures taper anterolaterally in the horizontal plane without a marked downward deflection.

(3) Coronoid process of mandible very deep, and formed of steep, slender processes of dentary and angular part of anguloarticular bones (Fig. 13B). The coronoid process is relatively much less prominent in other pimelodids and most other catfishes, including diplomystids and †hypsidorids (e.g., Lundberg & McDade 1986: fig. 9).

(4) “Cleithral ring” comprised of supracleithrum’s lateral and medial processes plus fourth transverse process that together surround dorsal limb of cleithrum (Fig. 12B cl. ring). Despite debate over the composition of the upper element of the catfish shoulder girdle, Lundberg (1975) and Fink & Fink (1981) would agree that the ventral part of the bone that articulates with the cleithrum should be termed supracleithrum. In most pimelodids, and catfishes generally, including diplomystids and †hypsidorids, the ventral part of the supracleithrum has a deep “cleithral notch” flanked by two parallel or

divergent processes that together clasp the pointed dorsal limb of the cleithrum (Fig. 12A cl. notch; see also Lundberg 1975: fig. 2B and C). Primitively, the two processes of the supracleithrum are unequally developed: the lateral process is the longer, whereas the medial process is shorter and has a major articulation site on its posterior surface for the expanded anterior limb of the transverse process of vertebra four. In the formation of the "cleithral ring" of the "*Calophysus-Pimelodus* clade," the fourth transverse process is drawn out posteriorly and converges on the medial surface of the supracleithrum's lateral process with which it has a firm, ligamentous union. Also, the supracleithrum's lateral process is drawn out posteroventrally to make contact with a flange of the cleithrum that projects dorsal to the otherwise concave posterior margin between the upper cleithral limb and posterior cleithral process.

"*Pimelodus* group."—Within the "*Calophysus-Pimelodus* clade" we have identified one putative synapomorphy for a monophyletic group including the nominal genera *Cheirocerus*, *Duopalatinus*, *Exallodontus*, *Iheringichthys*, *Parapimelodus*, *Pimelodus*, *Platysilurus*, and *Platystomatichthys*. The genera *Bagropsis*, *Bergiaria*, and *Conorhynchos* are tentatively included in this lineage based on external characters, but we have not examined skeletonized specimens. The synapomorphy supporting this clade is: transverse processes of vertebrae four and five are sutured to their lateral edges (Fig. 12B). This broad union of the transverse processes creates a longer and broader osseous sheet over the swimbladder than in any other pimelodids and most other catfishes, including diplomystids and †hypsodorids. Lundberg & McDade (1986) and Lundberg et al. (1991) described and illustrated various conditions of the form of the fourth, fifth and sixth transverse processes in the Pimelodidae. The primitive condition in the family, as identified by outgroup

comparison, is found in *Leiarius*, *Microglanis* (Lundberg & McDade 1986: fig. 4E), *Pseudopimelodus*, *Lophiosilurus* and *Zungaro* in all of which the posterior limb of the fourth transverse process tapers to a blunt tip, and there is a deep notch between this process and the much smaller fifth transverse process. In other pimelodid genera a distinct and usually deep notch between the fourth and fifth transverse processes is retained (Fig. 12A).

Within the "*Pimelodus* group" the relationships of *Bagropsis*, *Bergiaria*, and *Conorhynchos* have not been studied by us and are unresolved. The other genera of the group can be assigned to two smaller clades. The first clade includes *Platysilurus* and *Platystomatichthys* whose close relationship is indicated by two features that may be unique among catfishes: (1) narrow dorso-medial groove extending from posterior fontanelle across supraoccipital process onto anterior nuchal plate (supraneural), and (2) greatly hypertrophied maxillary bone that reaches, within its barbel, to about the anal fin origin. The second clade within the "*Pimelodus* group" contains *Cheirocerus*, *Duopalatinus*, *Exallodontus*, *Iheringichthys*, *Parapimelodus*, and *Pimelodus*. This alignment is suggested by the apomorphically extensive posterior development of superficial ossification of the Weberian complex centra that ventrally covers the seventh centrum (Fig. 12B). Other pimelodids (except one known to us) and most other siluriforms, including diplomystids and †hypsodorids, have the seventh centrum exposed ventrally and the superficial ossification restricted to more anterior vertebrae (Fig. 12A). The single exception among the pimelodids is *Brachyplatystoma rousseauxi* that has the seventh centrum completely covered by superficial ossification. We have interpreted this as a homoplasious similarity between *B. rousseauxi* and the "*Pimelodus* group." *B. rousseauxi* not only lacks the other synapomorphies of the "*Calophy-*

sus-Pimelodus clade" and the *Pimelodus* group, but instead shares several unique apomorphies with species currently classified in the nominal genera *Brachyplatystoma* and *Goslinia* (Nass, in prep.).

Pimelodus. — In the literature dating back to at least Eigenmann & Eigenmann (1888, 1890), *Exallodontus aguanai* would be identified as a species of *Pimelodus*. For the reasons given above we have chosen to describe *Exallodontus* as a new genus. Assignment of *E. aguanai* to *Pimelodus* would make a bad situation worse. *Pimelodus* has an old and complex taxonomic history involving catfishes from all over the world. Even restricted as it is now to a group of South American catfishes, *Pimelodus* is complex (e.g., *P. heteropleura* is a member of the Rhamdiinae, closely similar to *Brachyrhamdia* and *Pimelodella*), the species-level taxonomy of the species and populations similar to the type species *P. maculatus* is unsettled, and the genus has not been diagnosed in an explicit phylogenetic framework. A revision of *Pimelodus* is underway by D. J. Stewart.

Here we offer some data on a character complex that might prove useful in a phylogenetic diagnosis of *Pimelodus*. Most catfishes have a relatively simple pattern of trigeminofacial nerve foramina in the prootic and pterosphenoid in contrast to other otophysans and teleosts (Howes 1983). Our survey suggests that the majority of siluriform families have one large foramen on the prootic-pterosphenoid boundary (Fig. 14A), or rarely in the prootic alone, for the major branches of the fifth and seventh cranial nerves, i.e., the maxillary and mandibular branches of the trigeminal, and the hyomandibular and palatine trunks of the facial. Separate small foramina are usually present for the superficial ophthalmic branches of the fifth and seventh nerves. Diplomystids (also, Howes 1983, lists some other catfishes) have the single trigeminofacial foramen confluent with the optic foramen in the orbitosphenoid. The single trigeminofacial fo-

ramen is also the general condition for pimelodids, being found in the subfamilies Rhamdiinae and Pseudopimelodinae, and most Pimelodinae. In a few Pimelodinae, including *Calophysus* (Fig. 14B), *Goslinia*, *Hypophthalmus* (Howes 1983: fig. 17), *Pimelodina*, and *Sorubim*, the main branches of trigeminal and facial exit through their own separate foramina. Outside of the Pimelodidae the facial nerve foramen is subdivided in some silurids (*Belodontichthys*, *Kryptopterus*, *Silurus*). In several species of *Pimelodus* (*blochi*, *grosskopfi*, *coprophagus*, cf. *clarias* from the Río Magdalena, and *pictus*, but not *ornatus* or *altissimus*) there is an additional foramen (Fig. 14C). In these species there are three separate foramina, one each for the maxillary, mandibular and hyomandibular (facial) nerves. These species also have smaller foramina and canals through the prootic and pterosphenoid. Details of this complex anatomy remain to be worked out across a wide swath of pimelodids. At present it is clear, however, that many species of *Pimelodus* share an unusual derived condition of the trigeminofacial foramina. That *Exallodontus* lacks this feature and is like the majority of other pimelodids is consistent with our description of the genus as taxically distinct from *Pimelodus*.

Comments on some papers by Howes. — As noted above, Howes (1983) argued for a relationship of *Hypophthalmus* within the Pimelodidae. We agree and assign this highly specialized genus to the Pimelodinae. Howes (1983) also proposed "three major groups" of pimelodids and listed exemplar members and some characters for each. Howes' third group (*Rhamdia*, *Pimelodella*, *Heptapterus*) includes members of the Rhamdiinae (Lundberg & McDade 1986, Lundberg et al. 1991). The characters listed by Howes for this group are relatively plesiomorphic among pimelodids, i.e., unencapsulated swimbladder without caecae or compressor muscles, and five vertebrae included in the Weberian complex. Howes'

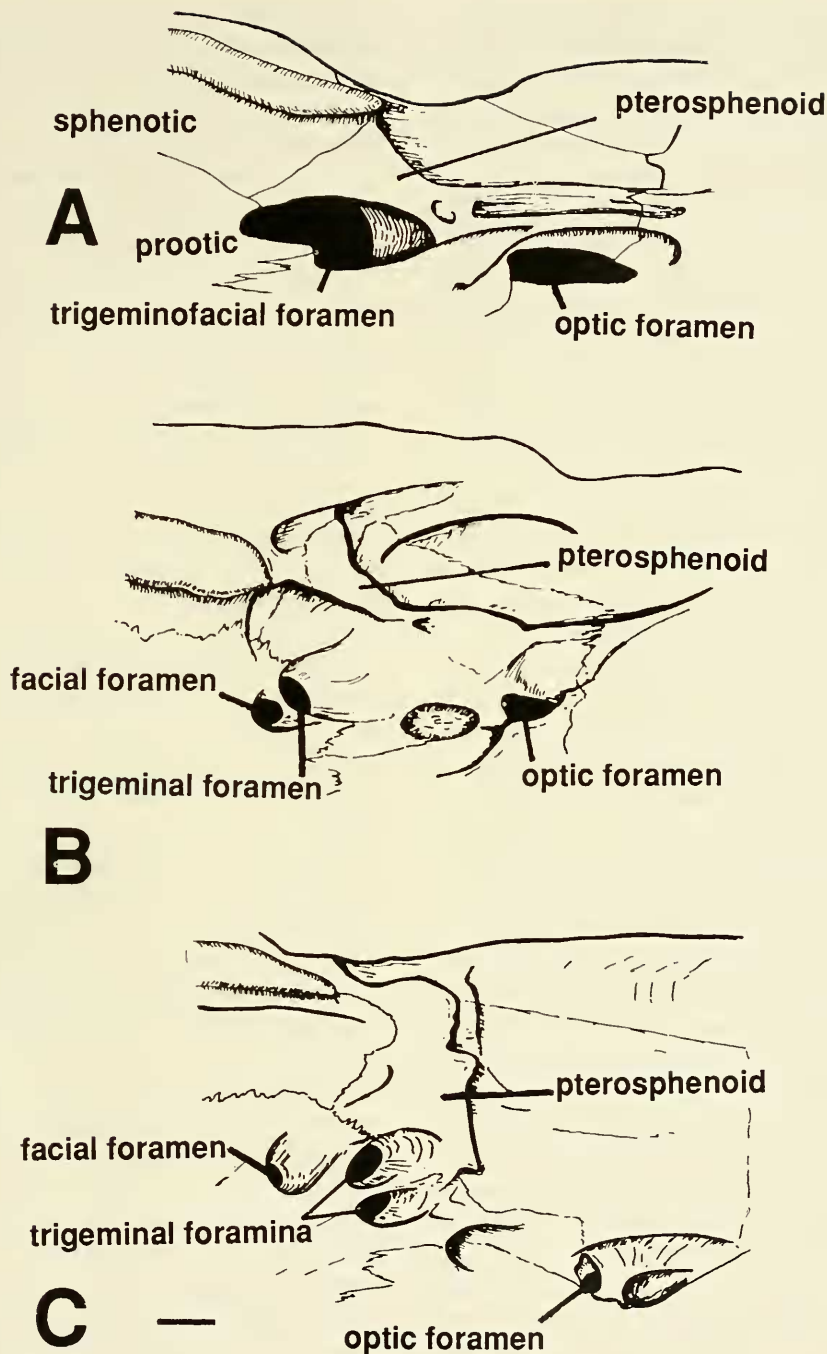


Fig. 14. Trigeminofacial foramina in A. *Rhamdia wagneri*, DU-F-1021, B. *Calophysus macropterus*, DU-F-985, C. *Pimelodus grosskopfii*, DU-F-919, Scale bar for A and C = 2 mm, for B = 1 mm.

first group (*Calophysus*, *Iheringichthys*, *Luciopimelodus*, *Megalonema*, *Parapimelodus*, *Pimelodina*, *Pinirampus*, *Pimelodus* (part)) plus his second (*Pseudoplatystoma*, *Hemisorubim*, *Sorubim*, *Pimelodus* (part)) include members of our "Group A" diagnosed, as above, by the aortic tunnel. The characters listed by Howes for his second group are also relatively plesiomorphic or uncertainly apomorphic among catfishes, i.e., unencapsulated swimbladder with muscular walls, and a maxillary barbel retractor muscle. Howes characterized his first group as having partially encapsulated swimbladder, but this is contradicted by our specimens of *Iheringichthys* and *Parapimelodus*, and we have not observed specimens of *Pimelodus* with such a condition. Otherwise this group corresponds with Stewart's "*Calophysus* group."

Howes (1983) also noted the presence of two oddly-shaped pterygoid bones anterior to the metapterygoid in some members of his first group: *Calophysus*, *Iheringichthys*, *Parapimelodus*, *Pinirampus*, and *Pimelodus maculatus*. These bones are a "scythe-shaped" medial element between the lateral ethmoid and palatine, and a slender rod-like element lateral to the palatine. Respectively, we would term these bones, following Regan (1911), entopterygoid (=mesopterygoid or endopterygoid) and ectopterygoid. We also find similarly shaped entopterygoid and ectopterygoid elements in *Cheirocerus*, *Duopalatinus*, *Exallodontus*, *Megalonema*, *Pimelodina*, and *Pimelodus* (all species examined). These genera plus the ones cited by Howes are members of the "*Calophysus-Pimelodus* clade," but this group is not strictly characterized by such pterygoid bones. *Platysilurus* and *Platystomatichthys*, members of the clade, have instead plate-like anterior pterygoid elements, and *Leiarius*, not a member of the clade, has the scythe-shaped and rod-like configuration. Various other conditions of the anterior pterygoid bones and associated tooth plates in the Pimelodinae remain to be described and their

distributions determined precisely. At present we do not employ the form of the pterygoid bones in diagnoses of pimelodine subgroups.

The terminology of the pterygoid elements has been problematical. In a recent paper on the homologies of catfish pterygoids Howes & Teugels (1989) concluded that the two anterior elements are fragmented parts of the entopterygoid or sesamoid bones formed in ligaments. Howes & Teugels (1989) consider the ectopterygoid and entopterygoid to be represented in catfishes by ventral and anterodorsal osseous laminae fused with the metapterygoid. Given current information this appears to be an unnecessarily complicated interpretation. From Howes & Teugels' (1989) developmental series of *Corydoras* (Callichthyidae), *Clarias* (Clariidae) and *Ageneiosus* (Ageneiosidae), and ours of *Pinirampus* (Pimelodidae), entopterygoid and ectopterygoid centers of ossification are not seen to form separately and then to fuse with the metapterygoid. Rather, as Howes & Teugels (1989) correctly describe, the metapterygoid begins as an endochondral bone on the pterygoquadrate cartilage and later anterodorsal and ventral laminae extend outward from it. This does not appear to be different from the endochondral quadrate and hyomandibula which in many catfishes develop membranous, laminar extensions into surrounding connective tissues. The most primitive form of the anterior pterygoids in siluriforms appears to be that of diplomystids, and here we disfavor Arratia's (1987) terminology for these as "additional pterygoid" and "bone 4 of McMurrich." In diplomystids there are two small toothless plates anterior to the metapterygoid, the more lateral of which is at the posterior tip of the palatine, in line with the main axis of the metapterygoid, and the other is offset medially. Although these bones are not in sutural contact they have the expected relative positions of ectopterygoid (more lateral and contacting the palatine) and entop-

terygoid (more medial). It is our belief that the most parsimonious interpretation of the scythe-shaped and rod-like elements of some pimelodids is that they are apomorphic conditions of the entopterygoid and ectopterygoid respectively but that their level of taxonomic generality within the subfamily Pimelodinae remains to be determined.

Comparative material examined.—Listed below are first, alcohol preserved specimens of pimelodines used in morphometric comparisons of *Exallodontus*, and, second, skeletal specimens by subfamilies of Pimelodidae and, lastly, other families.

Alcohol preserved specimens.—Number of specimens and range of standard lengths follow catalogue number. *Calophysus macropterus* DU-F-(JGL 30-78), 2, 168–175, Venezuela, Orinoco Delta region; DU-F-(JGL 19-78), 2, 141–155, Venezuela, Orinoco Delta region; *Duopalatinus emarginatus* USNM 44974, 1, 176, Brazil, Rio das Velhas; *Duopalatinus peruanus* ANSP 158185, 1, 139, Venezuela, Puerto Ayacucho; ANSP 160189, 3, 80–86, Venezuela, Amazonas; ANSP 160203, 1, 80, Venezuela, Amazonas; MBUCV-V-14991, 2, 113, Venezuela, Rio Arauca; *Pimelodina flavipinnis* DU-F-(T 77-79), 1, 141, Venezuela, Orinoco Delta region; DU-F-(HLR 40-79), 4, 129–232, Venezuela, Orinoco Delta region; DU-F-(HLR 22-79), 2, 85–123, Venezuela, Orinoco Delta region; “*Pimelodus* A” from the Orinoco, DU-F-(HLR 6-79), 4, 132–170, Venezuela, Orinoco Delta region; DU-F-(HLR 12-79), 2, 118–152, Venezuela, Orinoco Delta region; DU-F-(HLR 13-79), 1, 156, Venezuela, Orinoco Delta region; DU-F-(HLR 19-79), 1, 98, Venezuela, Orinoco Delta region; DU-F-(HLR 22-79), 1, 167, Venezuela, Orinoco Delta region; DU-F-(JGL 40-78), 3, 46–122, Venezuela, Orinoco Delta region; “*Pimelodus* cf. A” from the Amazon, FMNH 41508, 2, 121–135, Brazil, Pará; USNM 121857, 3, 115–145, Brazil, Belém; FMNH 52572, 1, 177, Brazil, Amazonas; IU 4266 (at CAS), 2, Peru, Pebas; CAS 6612, 1, Brazil, Belém;

CAS 6649, 2, Brazil, Belém; CAS 6650, 1, Brazil, Belém; CAS 6582, 1, Brazil, Belém; SU 22178 (at CAS), 22, Brazil, Pará; *Pimelodus altissimus* CAS 55369, Paratype, 1, 166, Peru, Río Ucayali; *Pimelodus altissimus* (a complex of species), MZUSP 24587, 5, 140–161, Brazil, Rio Acre; MNJR 4863, 1, 108, Brazil, Rio Madeira; SU 33386 (at CAS), 1, 93, Peru, Pebas; UMMZ 205085, 4, 98–146, and AMNH 40138, 2, 114–114, Bolivia, Río Marmore; ANSP 150171, 1, 95, Peru, Iquitos. USNM 124879, 2, 166–186, Río Ambiyacu; *Pimelodus blochi* DU-F-(JNB 90-78), 3, 85–103, Venezuela, Orinoco Delta region; DU-F-(JNB 47-78), 7, 68–200, Venezuela, Orinoco Delta region; DU-F-(JNB 95-79), 4, 96–143, Venezuela, Orinoco Delta region; *Pinirampus pinirampu* DU-F-(JNB 30-78), 1, 185, Venezuela, Orinoco Delta region.

Skeletal materials.—Following catalogue number, in parentheses, are number of specimens, type of preparation and standard length (or as indicated skull length) in mm, when available. Abbreviations for preparations of skeletal specimens: c&s—cleared and alizarin stained, diss—dissection, dry—dry skeleton, xr—radiograph.

Pimelodinae: Brachyplatystoma filamentosum DU F1052 (1, dry, ca. 220 skull length) Venezuela; DU F1079 (1, dry, ca. 200 skull length) Venezuela; DU F1080 (1, dry, ca. 200 skull length) Venezuela; *Brachyplatystoma juruense* DU F983 (1, dry, ca. 185) Venezuela; DU F1071 (1, dry, 590) Venezuela; MBUCV-V-ES13 (1, dry, 568) Venezuela; *Brachyplatystoma rousseauxi* DU F981 (1, dry, ca. 650) Venezuela; DU F1051 (1, dry, ca. 185 skull length) Venezuela; DU F1057 (1, dry, ca. 155 skull length) Venezuela; DU F1078 (1, dry, ca. 276 skull length) Venezuela; MBUCV-V-uncat. (1, dry, 132) Venezuela; MBUCV-V-uncat. (1, dry, ca. 270 skull length) Venezuela; *Brachyplatystoma vaillanti* DU F994 (dry), DU F1034 (1, dry, 370) Venezuela; MBUCV-V-CT235 (2, c&s, 114–116) Venezuela; MBUCV-V-uncat. (1, dry, 370)

- Venezuela; *Calophysus macropterus* DU F985 (1, dry, 403) Venezuela; DU F1009 (1, c&s, 128) Venezuela; DU F1049 (1, dry, 217) Venezuela; DU F1103 (1, dry, 405) Venezuela; MBUCV-V-CT102 (1, c&s, 212); *Cheirocerus abuelo* MBUCV-V-CT1 (1, c&s, 154) Venezuela; *Exallodontus aguanai* DU F977 (1, dry, ca. 166) Venezuela; DU F865 (1, c&s, 82) Venezuela; DU F1047 (1, dry, ca. 186) Venezuela; DU F1048 (1, dry, ca. 72) Venezuela; *Duopalatinus peruanus* ANSP 160189 (1, c&s, 83) Venezuela; *Goslinia platynema* DU F992 (1, dry, ca. 415) Venezuela; DU F993 (1, dry, 182 skull length) Venezuela; DU F1076 (1, dry, ca. 561) Venezuela; MBUCV-V-CT443 (1, c&s) Venezuela; MBUCV-V-uncat (1, dry, 767) Venezuela; *Hemisorubim platyrhynchus* MBUCV-V-CT196 (1, c&s, 89) Venezuela; MCZ uncat. (1, dry) Brazil; *Hypophthalmus edentatus* DU F931 (1, dry, 352) Venezuela; DU F1043 (1, dry, 380) Venezuela; DU F1044 (1, dry, 390) Venezuela; MBUCV-V-uncat. (1, dry, 230) Venezuela; *Itheringichthys labrosus* DU F1000 (1, c&s, 86) Argentina; *Leiarius marmoratus* DU F987 (1, dry, ca. 320) Venezuela; DU F1036 (1, dry, 240) Venezuela; DU F1037 (1, dry, 210) Venezuela; DU F1053 (1, dry, 226) Venezuela; DU F1054 (1, dry, 276) Venezuela; DU F1055 (1, dry, 208) Venezuela; DU F1056 (1, dry, 293) Venezuela; MBUCV-V-CT234 (1, c&s, 52) Venezuela; *Megalonema* cf. *xanthum* DU F1011 (1, c&s, 72) Venezuela; DU F1001 (1, c&s, 72) Venezuela; *Megalonema* sp. DU F998 (1, c&s, 82) Venezuela; *Parapimelodus nigribarbis* MCP 6959 (1, c&s, 94) Brazil; *Parapimelodus valenciennes* MCP 12969 (1, c&s, 97) Venezuela; *Paulicea lutkeni* DU F982 (1, dry, 375) Venezuela; MBUCV-V-ES25 (1, dry, 260) Venezuela; *Perrunichthys perruno* MBUCV-V-14178 (1, diss) Venezuela; *Phractocephalus hemiliopterus* DU F925 (1, dry, 265) Venezuela; MBUCV-V-CT328 (1, c&s, 159), MBUCV-V-uncat. (3, dry, 415–ca. 800) Venezuela; *Pimelodina flavipinnis* DU F989 (1, dry, 310) Venezuela; DU F1008 (1, c&s, 107) Venezuela; *Pimelodus* sp. (“*altipinnis*”) SU (at CAS) 54122 (1, dry, 35 skull length) Brazil; “*Pimelodus* A” (Orinoco) DU F1006 (1, c&s, 136) Venezuela; DU F1010 (1, c&s, 37) Venezuela; *Pimelodus altissimus* AMNH 40138 (1, c&s, 123) Bolivia; *Pimelodus blochi* DU F988 (3, dry, ca. 95–100) Venezuela; DU F1037 (1, dry, 210) Venezuela; DU F1077 (1, dry, ca. 214) Venezuela; DU F1094 (1, dry, ca. 80) Venezuela; DU F1096 (1, dry, ca. 70) Venezuela; DU F1101 (1, dry, ca. 72) Venezuela; MBUCV-V-CT242, CT243, CT244, CT284 (11, c&s, 24–93) Venezuela; *Pimelodus coprophagus* MBUCV-V-CT150 (2, c&s) Venezuela; *Pimelodus grosskopfi* DU F919 (dry) Colombia; *Pimelodus ornatus* MBUCV-V-CT145 (2, c&s, 104–110) Venezuela; *Pimelodus pictus* DU F866 (c&s), MBUCV-V-CT70 (2, c&s, 60–67) Venezuela; DU F1012 (1, c&s, 65) Venezuela; *Pimelodus* cf. *clarias* DU F922 (1, dry, 212) Colombia; *P. “grosskopfei”* DU F919 (1, dry, 220) Colombia; *Pinirampus pirinampu* DU F984 (1, dry, 470) Venezuela; DU F1143 (11, c&s, 10–56) Venezuela; MBUCV-V-CT97, CT142 (3, c&s, 78–93) Venezuela; MBUCV-V-ES14 (2, dry, 310–572) Venezuela; *Platynemachthys notatus* MBUCV-V-uncat. (1, dry, 462) Venezuela; *Platysilurus* sp. DU F986 (1, dry, 186); DU F921 (1, dry, 230) Venezuela; MBUCV-V-CT92 (2, c&s, 86–102) Venezuela; *Platystomatichthys sturio* MBUCV-V-CT111 (1, c&s, 64) Venezuela; SU 22463 (at CAS) (1, dry, 96 skull length) Brazil; *Pseudoplatystoma faciatum* DU F864 (1, dry) Venezuela; DU F990 (1, dry, 970) Venezuela; DU F991 (1, dry, 258) Venezuela; DU F1060 (1, c&s, ca. 316) Venezuela; DU F1098 (1, dry, 215 skull length) Venezuela; DU F1100 (1, dry, ca. 395) Venezuela; DU F1125 (1, dry, ca. 240 skull length) Venezuela; MBUCV-V-CT489, CT491, CT492 (3, c&s, 25–66) Venezuela; MBUCV-V-ES17, uncat. (3, dry, 165–523) Venezuela; *Pseudoplatystoma tigrinum* DU F921 (1, dry, 230) Venezuela; DU F997 (1,

dry, 275 skull length) Venezuela; DU F1099 (1, dry, ca. 335) Venezuela; MBUCV-V-ES16 (1, dry, 557) Venezuela; MBUCV-V-CT uncat. (1, c&s, 25) Venezuela; *Sorubim lima* MBUCV-V-CT91, CT105, CT114 (2, c&s, 38–140) Venezuela; MBUCV-V-ES8 (4, dry, 195–226) Venezuela; *Sorubim* sp. DU F923 (1, dry, 336) Colombia; DU F1095 (1, dry, 195) Venezuela; *Sorubim* sp. MBUCV-V-uncat. (1, dry, ca. 500) Venezuela; *Sorubimichthys planiceps* MBUCV-V-CT505 (1, c&s) Venezuela; MBUCV-V-uncat. (1, dry, 265 skull length) Venezuela; *Steindachneridion parahybae* MCZ 25522 (1, dry) Brazil; MCZ 25523 (1, dry) Brazil.

Pseudopimelodinae: *Lophiosilurus alexandri* FMNH 95987 (1, c&s, 83) Brazil; *Microglanis poecilus* DU F1014 (3, c&s, 26–27) Venezuela; FMNH 9478 (4, c&s, 22–24) Venezuela; *Microglanis secundus* MBUCV-V-CT94 (3, c&s, 31–34) Venezuela; *Pseudopimelodus apurensis* DU F924 (1, dry, 430) Venezuela; DU F980 (1, dry, ca. 350) Venezuela; MBUCV-V-ES12 (1, dry, 418) Venezuela; DU-F1040 (1, dry, 285) Venezuela; *Pseudopimelodus raninus* MBUCV-V-CT95 (3, c&s, 58–72) Venezuela; *Pseudopimelodus* sp. DU F1102 (1, dry, ca. 75) Venezuela; *Pseudopimelodus* sp. MBUCV-V-CT222 (3, c&s, 30–52) Venezuela; *Zungaro zungaro* DU F920 (1, dry, 207) Colombia.

Rhamdiinae: *Acentronichthys leptos* FMNH 56902 (1, c&s, 37) Brazil; *Brachyglanis magoi* MBUCV-V-2600, CT139 (2, c&s, 48–50) Venezuela; MBUCV-V-uncat. (1, diss) Venezuela; *Brachyglanis melas* MBUCV-V-15919 (1, xr) Venezuela; *Brachyglanis* sp. AMNH 74394 (1, c&s) Venezuela; *Brachyrhamdia imitator* ANSP 139850 (2, c&s, 40) Venezuela; DU F1144 (2, c&s, 36–41) Venezuela; *Cetopsorhamdia picklei* MBUCV-V-CT98, CT138, CT264 (3, c&s, 56–65) Venezuela; *Cetopsorhamdia rosae* ANSP 137968 (c&s); *Cetopsorhamdia* sp. ROM ACC5056-RC86-42 (1, c&s, 49) Peru; *Chasmocranus longior* MBUCV-V-9817 CT137 (4, c&s, 28–56); *Chasmocra-*

nus sp. DU F1005 (2, c&s, 22–25) Venezuela; DU F1002A (1, c&s, 27) Venezuela; ANSP 165353 (2, c&s, 57–58) Venezuela; *Gladioglanis conquistador* FMNH 94973 (5, c&s, 27–32) Ecuador; *Gladioglanis machadoi* DU F1001 (1, c&s, 28), MBUCV-V-7293 (2, c&s, 23–26) Venezuela; FMNH 94793 (5, c&s, 20–28) Colombia; *Goeldiella eques* AMNH 13669 (c&s); *Heptapterus mustelinus* FMNH 56897 (1, c&s, 49) Brazil; *Heptapterus* sp. FMNH 83860 (1, c&s, 76); DU F1002B (1, c&s, 30) Venezuela; *Imparales panamensis* USNM 308587 (1, c&s, 54) Panama; *Imparfinis* sp. ANSP 135899 (c&s); ANSP 149927 (1, c&s, 43); *Imparfinis* sp. ROM ACC5056-RC86-31 (1, c&s, 62) Peru; *Leptorhamdia essequibensis* MBUCV-V-6959 (X); *Leptorhamdia* cf. *marmoratus* AMNH 74403 (c&s) Venezuela; *Medemichthys guayaberensis* ICN-NHM uncat. (2, c&s, 30–31) Colombia; *Myoglanis* sp. MBUCV-V-CT78 (1, c&s, 70) Venezuela; *Myoglanis* sp. AMNH 74407 (c&s); *Nannorhamdia nemacheir* DU F1004 (1, c&s, 25) Venezuela; USNM 121163 (1, c&s, 54) Venezuela; *Nannorhamdia pseudonemacheir* DU F1003 (3, c&s, 31–32) Venezuela; *Nannorhamdia* sp. MBUCV-V-14257 (1, c&s, 37) Venezuela; *Nannorhamdia* sp. MBUCV-V-14264 (1, c&s 49) Venezuela; *Nannorhamdia* sp. MBUCV-V-14346 (1, c&s, 34) Venezuela; *Nannorhamdia* sp. MBUCV-V-14464 (1, c&s, 32) Venezuela; *Nannorhamdia* sp. MBUCV-V-9215 (c&s); *Pariolius armillatus* ANSP 130596 (1, c&s, 35) Peru; *Pariolius fasciatus* ANSP 128696 (c&s); *Pariolius* sp. ANSP 178696 (2, c&s, 34–36); *Pimelodella chagresi* USNM 308586 (1, c&s, 82) Panama; *Pimelodella cristata* MBUCV-V-CT93, CT575, CT576 (4, c&s, 129–166) Venezuela; *Pimelodella hasemani* DU F1007 (3, c&s, 43–46) Venezuela; *Pimelodella metae* MBUCV-V-CT526, CT528 (3, c&s, 64–99) Venezuela; *Pimelodella* sp. DU F979 (1, dry, ca. 80) Venezuela; DU F1013 (1, c&s, 88) Venezuela; DU F1097 (2, dry, 55–92) Venezuela; DU F1104 (1, dry, 85) Venezuela; Rhamdiinae

gen. et sp. indet. MBUCV-V-9215 (1, c&s, 60) Venezuela; "*Pimelodus*" (cf *Brachyrhamdia heteropleura* AMNH 52410 (2, c&s, 38); *Rhamdella* sp. MBUCV-V-CT190 (1, c&s, 119) Venezuela; USNM 270038 (c&s); *Rhamdia quelen* MBUCV-V-CT214, CT215, CT291, CT296 (7, c&s, 101–126) Venezuela; MBUCV-V-ES15 (3, dry, ca. 245) Venezuela; *Rhamdia sebae* DU F861 (1, c&s, 57) Venezuela; *Rhamdia wagneri* DU F1021 (1, dry, 204) Panama; *Rhamdia* sp. DU F978 (3, dry, ca. 95–100) Venezuela; *Rhamdia* sp. MBUCV-V-14048 (1, c&s) Venezuela; *Rhamdia* sp. USNM 270038 (1, c&s, 110) Venezuela.

Other siluriforms: Ageneiosidae: *Ageneiosus brevifilis* DU F927 (1, dry, 133) Venezuela; MBUCV-V-uncat. (1, dry, 350) Venezuela; *Ageneiosus ucayalensis* DU F928 (1, dry, 226) Venezuela; DU F1068 (1, dry, 316) Venezuela; *Ageneiosus* sp. DU F1145 (1, c&s, 60) Venezuela; Akysidae: *Acrocordontichthys melanogaster* FMNH 68010 (1, c&s, 38) Borneo; *Akysis* sp. UMMZ 214905 (1, c&s, 36) Vietnam; Amblycipitidae: *Amblyceps mangois* UMMZ 208651 (1, c&s, 35) Bangladesh; *Liobagrus andersoni* DU F1108 (2, c&s, 86–90) Korea; *Liobagrus formosanus* DU F1116 (1, c&s, 75) Taiwan; DU F1117 (1, c&s, 78) Taiwan; *Liobagrus mediadiposalis* DU F1109 (1, c&s, 82) Korea; DU F1111 (1, c&s, 83) Korea; *Liobagrus obesus* DU F1110 (2, c&s, 80–90) Korea; *Liobagrus xiurenensis* DU F1124 (1, c&s, 90) China; Amphiliidae: *Amphilius jacksoni* UMMZ 199987 (2, c&s, 32–85) Zambia; Ariidae: *Ariopsis seemani* DU F1017 (1, dry, 243) Panama; DU F1019 (1, dry, 130) Panama; *Arius felis* DU F995 (1, dry, 175) North Carolina; *Arius jordani* DU F1020 (1, dry, 210) Panama; *Arius kessleri* DU F1015 (1, dry, 320) Panama; DU F1016 (1, dry, 165) Panama; *Arius proops* USNM 214860 (1, dry) Colombia; *Bagre panamensis* DU F1018 (1, dry, 210) Panama; *Potamarius nelsoni* UMMZ 143496 (1, dry) Guatemala; *Sciadops troscheli* USNM 214864 (1, dry) Colombia; Aspredinidae: *Agmus lyriformis*

USNM 226079 (2, c&s, 56–62) Surinam; *Xyliphius* sp. DU F999 (1, dry, 64) Venezuela; *Bunocephalus* sp. DU F940 (1, dry, 94) aquarium spec.; Auchenipteridae: *Entomocorus benjamini* DU F1146 (2, c&s, 50–52) Venezuela; *Trachycorytes striatulus* SU (at CAS) 2151 (1, dry, 102) Brazil; Bagridae: *Bagroides malapterus* UMMZ 155695 (1, c&s, 87) Sumatra; *Bagrus ubangensis* SU (at CAS) 54218 (1, dry) Africa; *Chrysichthys furcatus* SU (at CAS) 54219 (1, dry) Africa; *Chrysichthys punctatus* SU (at CAS) 54220 (1, dry) Africa; *Chrysichthys walkeri* UMMZ 187901 (2, c&s, 57–65) Sierra Leone; *Coreobagrus ichikawai* UMMZ 187544 (1, c&s, 62) Japan; *Liocassis siamensis* UMMZ 186730 (2, c&s, 42–56) Thailand; *Mystus cavasius* UMMZ 186731 (1, c&s, 59) Thailand; *Mystus gulio* UMMZ 186724 (1, c&s, 55) Thailand; *Mystus nemurus* UMMZ 186685 (1, c&s, 50) Thailand; *Mystus vittatus* UMMZ 186780 (1, c&s, 63) Thailand; *Mystus wijcki* UMMZ 186785 (1, dry) Thailand; *Pelteobagrus nudiceps* UMMZ 187592 (1, dry, 166) Japan; *Pseudobagrus adiposalis* DU F1121 (1, c&s, 115) China; *Pseudobagrus aurantiacus* UMMZ 183870 (1, c&s, 65) Japan; Callichthyidae: *Corydoras* sp. DU F1147 (2, c&s, 38) Aquarium spec.; *Hoplosternum thoracatum* DU F1061 (1, dry, 169) Venezuela; DU F1062 (1, dry, 152) Venezuela; FMNH 84055 (2, c&s, 50–60) Colombia; *Hoplosternum littorale* MBUCV-V-ES003 (1, dry, ca. 250) Venezuela; Cetopsidae: *Cetopsis coecutiens* SU (at CAS) 54120 (1, dry) South America; *Paracetopsis occidentalis* SU (at CAS) 54120 (1, dry) Ecuador; Chacidae: *Chaca* sp. DU F1148 (1, dry, 80) Aquarium spec.; Clariidae: *Clarias batrachus* MBUCV-V-CT159 (1, c&s, 68) Venezuela; *Clarias gariepinus* UMMZ 200087 (1, dry, 300) Zambia; *Clarias ngamensis* UMMZ 200273 (2, dry, 258–279) Zambia; Cranoglanididae: *Cranoglanis multiradiatus* DU F917 (1, c&s, 56) China (PRC); Diplomystidae: *Diplomystes chilensis* MBUCV-V-CT585 (1, c&s) Chile; *Diplomystes papillosus* MCZ 8920 (1, c&s)

- Chile; *Olivaichthys viedmensis* DU F913 (1, c&s, 115) Argentina; Doradidae: *Leptodoras* sp. DU F847 (1, c&s, 105) Venezuela; *Megalodoras iriwini* DU F925 (1, dry, 133) Venezuela; DU F996 (1, dry) Venezuela; DU F1041 (1, dry, 430) Venezuela; DU F1045 (1, dry, 440) Venezuela; DU F1069 (1, dry, ca. 345) Venezuela; DU F1126 (1, dry, 345) Venezuela; *Orinocodoras eigenmanni* DU F926 (1, dry, 198) Venezuela; *Platydoras costatus* DU F1105 (1, dry, 118) Venezuela; DU F1106 (1, dry, ca. 111) Venezuela; *Pseudodoras niger* DU F1092 (1, dry, 154 skull length) Venezuela; MBUCV-V-ES uncat. (1, dry, 170) Venezuela; *Pterodoras angeli* DU F1128 (1, dry, 83) Venezuela; MBUCV-V-ES uncat. (1, dry, 250) Venezuela; m spec.; Helogenidae: *Helogenes maroratus* MBUCV-V-CT165 (2, c&s, 48–58) Venezuela; Heteropneustidae: *Heteropneustes fossilis* MBUCV-V-CT181 (1, c&s) India; †Hypsidoridae: †*Hypsidoris farsonensis* PU 20570, FMNH PF 10453 (1, fossil and cast, 169) Wyoming; Ictaluridae: *Ameiurus brunneus* DU F915 (2, dry, 139–145) North Carolina; DU F1137 (1, c&s, 59) North Carolina; UMMZ 186241-S4 (1, dry, 230) North Carolina; *Ameiurus catus* UMMZ 186242-S1 (1, dry, 287) North Carolina; *Amiurus melas* FMNH 42076 (2, c&s, 42–74) Illinois; UMMZ 189296-S1 (1, dry) Kansas; *Ameiurus natalis* DU F916 (2, c&s, 77–85) North Carolina; DU F1135 (1, c&s, 35) North Carolina; UMMZ 182060-S1 (1, dry, 228) Michigan; *Ameiurus nebulosus* DU F1129 (1, dry, 245) North Carolina; DU F1133 (1, c&s, 32) North Carolina; DU F1138 (1, c&s, 63) North Carolina; UMMZ 182047-S1 (1, dry, 234) Michigan; *Ameiurus platycephalus* UMMZ 186254-S2 (1, dry, 202) South Carolina; *Ameiurus serracanthus* UMMZ 186258-S4 (1, dry, 180) Florida; †*Astephus antiquus* FMNH PF1035a,b (1, fossil, 71) Wyoming; USNM 8122 (1, fossil, 230) Wyoming; *Ictalurus furcatus* UMMZ 169031-S5 (1, dry, 327) Missouri; *Ictalurus punctatus* DU F930 (2, c&s, 50–51) North Carolina; DU F1081 (1, c&s, ca. 197) pond raised; UMMZ 186271 (1, dry, 304) Mississippi; DU F1131 (1, c&s, 43) North Carolina; DU F1134 (1, c&s, 42) aquarium; *Noturus flavus* UMMZ 126365 (1, dry, 224) Ohio; *Noturus furiosus* DU F1136 (2, c&s, 46–46) North Carolina; DU F1139 (1, c&s, 62) North Carolina; *Noturus gyrinus* DU F1132 (1, c&s, 50) North Carolina; *Noturus insignis* DU F1130 (2, c&s, 40–45) North Carolina; DU F1140 (1, c&s, 73) North Carolina; DU F1141 (1, c&s, 66) North Carolina; DU F1142 (2, c&s, 30–32) North Carolina; DU F1143 (5, c&s, 94–110) North Carolina; *Noturus stigmosus* UMMZ 165841-S1 (1, dry, 87) Michigan; *Prietella phreatophila* UMMZ 173788 (1, c&s) Mexico; *Pylodictis olivaris* UMMZ 169029 (1, dry, 306) Missouri; *Satan eurystomus* Hubbs and Bailey: WMM (Witte Memorial Museum) 34-20-7, G (1, xr, 69) Texas; *Trogloglanis pattersoni* SIOH 51-379-18A (1, c&s) Texas; Loricariidae: *Acanthicus histrix* DU F1093 (1, dry, ca. 420) Venezuela; *Loricaria* sp. DU F1066 (1, dry, 263) Venezuela; DU F1127 (2, dry, 175–195) Venezuela; *Panaque* sp. DU F1067 (1, dry, 242) Venezuela; *Sturisoma* sp. DU F1064 (1, dry, ca. 294) Venezuela; DU F1065 (1, dry, 215) Venezuela; Malapteruridae: *M. electricus* MBUCV-V-CT335 (1, c&s, 65) Africa; USNM 118777 (1, c&s, 79) Liberia; *Malapterurus microstoma* USNM 265121 (1, dry, 520) Aquarium spec.; Mochokidae: *Atopocheilus* sp. CAS 47458 (1, dry) Africa; *Euchilichthys* sp. SU (at CAS) 54221 (1, dry) Africa; *Synodontis longirostris* SU (at CAS) 54222 (1, dry) Africa; *Synodontis membranaceus* MBUCV-V-CT171 (1, c&s) Africa; Nematogeneidae: *Nematogenys inermis* Guichenot IUM 15060 (1, c&s) Chile; Olyridae: *O. longicaudata* UMMZ 208811 (1, c&s, 85) Bangladesh; *Olyra* sp. CAS 54502 (1, c&s, 54) Thailand; Pangasiidae: *Pangasius* sp. DU F907 (1, dry, 250) Thailand; Plotosidae: *Plotosus canius* UMMZ 155790 (1, dry, 255) Indonesia; Schilbeidae: *Eutropius congensis* SU (at CAS) 54135 (1, dry, 195) Zaire; *Helicopha-*

gus waandersi UMMZ 186797 (2, c&s, 77–117) Thailand; *Laides hexanema* UMMZ 186798 (1, c&s, 65) Thailand; *Schilbe mystus* MBUCV-V-174 (1, c&s) Africa; UMMZ 187334 (1, dry) Uganda; UMMZ 200118 (1, dry, 305) Zambia; Siluridae: *Belodontichthys dinema* DU F-906 (1, dry, 370) Thailand; *Hemisilurus mekongensis* DU F-904 (1, dry, 422) Thailand; *Kryptopterus bicirrhys* DU F-912 (1, c&s, 42) aquarium specimen; *Parasilurus asotus* DU F-908 (1, dry, 320) China; DU F-929 (1, c&s, 130) No data; *Parasilurus grahami* DU F-911 (1, dry, 382) China; *Silurus cochinchinensis* DU F-909 (1, c&s, 93) No data; DU F-910 (1, c&s, 93) No data; *Wallago attu* DU F905 (1, dry, 506) Pakistan; Sisoridae: *Bagarius bagarius* UMMZ 186793 (1, c&s, 90) Thailand; *Erethistes pusillus* UMMZ 208697 (1, c&s, 36) Bangladesh; *Gagata cenia* UMMZ 208281 (1, c&s, 41) Bangladesh; UMMZ 208356 (1, c&s, 46) Bangladesh; *Glyptothorax ribeiroi* UMMZ 208955 (1, c&s, 26) Bangladesh; *Glyptothorax shawi* UMMZ 208967 (1, c&s, 24) Bangladesh; *Glyptothorax trilineatus* UMMZ 186849; *Hara hara* UMMZ 208748 (1, c&s, 50) Bangladesh; *Hara jerdoni* UMMZ 208401 (1, c&s, 20) Bangladesh; Trichomycteridae: *Trichomycterus* sp. FMNH 96618 (1, c&s, 104) Ecuador.

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